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Assessment and prediction of the potential threats of temperature change and invasive species to the sustainability of Northern Irish sea fisheries

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Assessment and prediction of the potential threats of temperature change and invasive species to the sustainability of Northern Irish sea fisheries

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Josie South, BSc.

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Declaration

I declare that the work contained within this document was carried out in accordance with the regulations of the Queen's University Belfast and complies with the criteria required by the Academic Council as follows:

(i) The thesis is not one for which a degree has been or will be conferred by any other university of institution.

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(iii) The work for the thesis is my own and that, where material submitted from another degree or work undertaken by another party as part of a research group has been incorporated into the thesis, the extent of that work thus incorporated has been clearly indicated.

(iv) The composition of the thesis is my own work.

(v) Any views expressed in the thesis are those of the author and in no way represent those of Queen's University Belfast.

Josie South

October 2017

Publications

The following work from this thesis has been published:

South, J., Dick, J.T.A., McCard, M., Barrios-O'Neill, D., Anton, A. (2017). Predicting predatory impact of juvenile invasive lionfish (*Pterois volitan*s) on a crustacean prey using functional response analysis: effects of temperature, habitat complexity and light regimes. *Environmental Biology of Fishes,* 1–11. doi:10.1007/s10641-017-0633-y

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Abstract

Understanding and predicting the way in which species interactions may change under the uncertain climatic future is imperative if the management of important resources is to be successful. Consumer – resource interactions underlie population dynamics and distribution, yet there is little known about how these interactions will respond to increasing temperature. Temperature increase can facilitate the movement and settlement of alien species into new ranges. Introduced species can often be ecologically damaging and unpredictable due to novel predator-prey interactions. Comparative functional response analysis has been used to gain insight into resource dependent behaviour and population dynamics. This study is an assessment of the way in which predicted temperature changes can affect resource consumption in three predators. The red lionfish *Pterois volitans* (Linnaeus, 1758) is a successful and hugely damaging invader in the Western Atlantic and sources point to an ongoing Mediterranean invasion. Through a series of laboratory experiments I assessed how temperature, habitat complexity, and light wavelength affect the functional response of lionfish towards a crustacean prey. I establish that lionfish have a persistent Type II functional response and that lower temperature decreased the magnitude of the functional response, suggesting that movement into the comparatively colder waters of the Mediterranean and British Isles could reduce the *per capita* response. Further, I found that red light reduced the maximum feeding rate of lionfish, compared to blue and white light, by dampening the attack rate. I assessed how temperature increase affects the proportional consumption of an amphipod prey by an intertidal predator, the bleniid, *Lipophrys pholis* (Linnaeus, 1758). Functional response analysis revealed that the shanny has a hump shaped relationship with increasing temperature wherein maximum feeding rate decreased at the highest temperature. Two prey supply models, where prey density was allowed to deplete, and where prey were replaced after consumption were compared and found to have differential results due to model choice. I used gut content data to assess the abundance, prey selection, degree of dietary overlap, in a commercial predator, cod (*Gadhus morhua*; Linnaeus, 1758) and a non-commercial predator, dogfish (*Sycliorhinus canicula*; Linnaeus, 1758) with regards to substrate type. While there were no significant conclusions to be made about habitat use, I found significantly larger populations of *S. canicula* and higher consumption of commercial invertebrates by *S. canicula.* I

used this field data to inform further experiments, having highlighted *S. canicula* as a potential threat to commercial fisheries. A two-by-two experimental design was used to understand how differential acclimation of predator (*S. canicula*) and amphipod prey species (*Echinogammarus marinus*; Leach, 1815) affects the functional response of the predator. Increasing temperature concomitantly increased the magnitude functional response of *S. canicula,* however raised temperature caused a shift in functional response type, from Type II to Type III, conferring low prey density protection. Handling time was shorter when both predator and prey were acclimated to the raised temperature and as a result there was a significant interaction effect where maximum feeding rate was significantly higher when both predator and prey were acclimated. This increase in predation impact by *S. canicula* has the potential to affect valuable fisheries stocks due to the increasing populations of *Scyliorhinus canicula* and the additive effects of acclimation to raised temperature. Having highlighted the differential ways in which temperature can affect the *per capita* response of consumers I postulate a new metric wherein "Relative Impact Potential" of a consumer can be predicted under a set of environmental variables. This metric takes into account the *per capita* response, numerical response, and the potential change in predator and prey populations under the proposed conditions. I suggest the use of this metric as a rapid way of assessing and predicting potential threats to sustainability of fisheries under predicted climatic change. Overall, this thesis identifies species and scenarios wherein sustainability of important fisheries could be threatened. While this work focuses mainly on thermal responses, it demonstrates: (i) the utility of functional response analysis in assessing relative change in ecological impact under climate change scenarios; (ii) the species specificity of thermal responses and provides empiricle evidence of a hump shaped thermal response; (iii) the importance of considering both predator and prey when assessing ecological change, with reference to acclimation and population dynamics; and (iv) a metric with which to assess potential threats and ecological impact in a way that is standardized and easily accessible by managers and stakeholders alike.

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Chapter 1

General Introduction

1.1 Climate Change

The Convention on Climate Change (UNFCCC 1992) (Article 1), defines climate change as:

"A change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods."

Radiativeforcing by greenhouse gases is the primary cause of climatic change (Collins *et al*. 2013; Trenberth *et al*. 2014; von Schuckman *et al*. 2016). It is estimated that the oceans have absorbed around 90% of this energy (Trenberth *et al*. 2014; Cheng *et al*. 2016), resulting in an increase in oceanic temperature (Bindoff *et al*. 2007; Abraham *et al*. 2013; Peyser *et al.* 2016). The average temperature of the upper ocean has increased by 0.6°C in the last 100 years (Rhein *et al*. 2013) and is predicted to rise by a further 2°C by 2100 (Collins *et al*. 2013) under the Representative Concentration Pathway (RCP) 4.5 scenario (Thompson *et al*. 2011), which represents climate response to the stabilising of anthropogenic forcing.

Climatic change causes variation in the marine environment. This manifests as changes in abiotic parameters, causing temperature change (Collins *et al*. 2013), ocean acidification (Dore *et al*. 2009; Edenhofer *et al*. 2009), decreasing oxygen concentration (Stramma *et al*. 2008; Keeling *et al*. 2010), and stratification (Stramma *et al*. 2002; Olbert *et al*. 2012). Each of these factors will have indirect and direct effects on biological communities and eventually ecosystem functions that we rely upon (Duarte 2002; Garcia & Rosenberg 2010; Doney *et al*. 2012; Collins *et al*. 2013).

Changing parameters facilitate species movement and relocation (Perry *et al*. 2005; Rahel & Olden 2008; Walther *et al*. 2009; Mellin *et al*. 2016). The North Sea saw a 50% increase in species richness between 1986-2005 as a direct result of temperature increase and the subsequent translocation of small tropical species, along with 70% of species showing a shift in distribution and abundance (Perry *et al*. 2005; Simpson *et al*. 2011). Smaller scale effects include the homogenization of marine communities as interaction strengths become skewed (Sanford 1999; O'Connor *et al*. 2009) and systems become oligotrophic (Doney *et al*. 2012). Novel

communities and parameters incite novel species interactions that can be direct i.e. predator-prey interactions (Alexander *et al*. 2014; Côté *et al*. 2014; Cheng *et al*. 2017), or indirect trait mediated interactions (Shinen *et al*. 2009; Miller *et al*. 2014). These indirect interactions exert measurable change on community populations and can cause considerable damage (Côté *et al*. 2013; Paolucci *et al*. 2013; Iacarella *et al*. 2017). Invasion ecology and effects are discussed further, below.

Abiotic variables affect species directly in a number of ways. Temperature can decrease spermatozoan function in numerous fish species (Dadras *et al*. 2017) and decrease the success of reproductive traits in anemonefish (*Amphiprion melanopus*) (Miller *et al*. 2015). Live pteropods were not able to compensate for lost calcium carbonate under increased carbon dioxide concentrations and this led to a change in weight due to a decrease in calcification and active corrosion (Bednaršek *et al*. 2012). Studies by Kurihara & Shirayama (2004) and Clark *et al*. (2009) found that increasing carbon dioxide concentrations negatively influence the development of pluteus larvae. Donelson *et al*. (2014) demonstrated that exposure to temperature increases caused a decline in swimming and foraging performance in the tropical damselfish (*Acanthochromis polyacanthus*) but there is a potential for generational acclimation. Acclimation to increased temperature caused cortisol increase in haddock and cod and this has implications for disease susceptibility and decreased fitness (King *et al*. 2006). Varying temperatures can cause problems for larval development, as this can make it impossible for cod larvae to develop into crucial life history stages (Hiscock *et al*. 2004). Cod that were acclimated to higher temperatures returned to their usual cortisol levels faster than those at low temperatures (Barton & Schreck, 1987; King *et al*. 2006). Therefore, acclimation to higher temperatures can reduce the total magnitude of the stress response (Lankford *et al*. 2003; Vucic-Pestic *et al*. 2011; Sentis *et al*. 2015).

Behaviour is also affected by changes in the abiotic environment. Welch *et al*. (2014) investigated whether there was scope for transgenerational acclimation to carbon dioxide levels. Unlike temperature effects (Donelson *et al*. 2014), there was little potential for acclimation and it would be necessary for genetic adaptation to overcome the effects of increasing carbon dioxide in our oceans (Welch *et al*. 2014). Temperature increase mitigates chemical alarm cues elicited by poorly-fed fish to other conspecifics, compared to when the fish were well fed, this has implications for changes in food supply and predator-prey interactions (Lienart *et al*. 2016). Juvenile

fish lose their innate avoidance of chemical alarm cues. This suggests impairment of sensory performance and would have inevitable knock on consequences for predator-prey interactions (Welch *et al*. 2014). Similar reduction in anti-predator behaviour has also been documented in the urchin species *Diadema antillarum* in response to temperature increase (Bodmer *et al*. 2017). Temperature also has significant effects on the maximum feeding rates of organisms, wherein it may increase or decrease consumption (Dell, Pawar & Savage 2011; Paaijmans *et al*. 2013; Iacarella *et al*. 2015; Vasseur *et al*. 2014). Gilbert *et al*. (2014) propose that with an increase in temperature there should be an increase in foraging demand due to the subsequent energy deficiency due to increased metabolic rate; this may manifest as increased risk taking behaviour. Growth rates change with increases in temperature (Pörtner and Knust 2007), however, there is a trade-off where somatic tissue growth is inhibited due to an increase in metabolic rate and decrease in oxygen concentration (Jobling 1981; Jobling *et al. 1994*). This is predicted to cause decreasing predator biomass (Fussman *et al*. 2014; Sentis *et al*. 2017).

There are multiple stressors on the world's fisheries and as such it is necessary to understand how populations react to them in order to maintain fisheries sustainability in a changing climate (Brodziak & Link 2002; Crain *et al*. 2008; Williams *et al*. 2008; Gilman *et al*. 2010). It is clear that the effects of climate change are complex and diverse between taxonomic groups and populations (Helmuth 2002; Broitman *et al*. 2009; Englund *et al*. 2011; Calosi *et al*. 2013; Pinnegar *et al*. 2016). These are highly likely to cause change in populations and community assemblages, which may have negative or positive implications for economic and ecological resources (Cinner *et al*. 2016; O'Gorman *et al*. 2016). Novel techniques need to be implemented to quantify biological interactions under predicted scenarios (Van der Putten *et al*. 2010). I address this in Chapter 6. Throughout this thesis I focus on temperature as a driving factor due to it being highly pervasive, affecting metabolic processes (Arrhenius 1889; Brown *et al*. 2004), and due to the potential for acclimation (Miller *et al*. 2015, Sentis *et al*. 2015; Donelson *et al*. 2016) (Chapters 2, 3, 5, 6).

1.2 Invasive Species

A biological invasion is the human mediated movement of a species into a recipient novel ecosystem where it thrives and often has a detrimental effect on the native community (Mack *et al*. 2000; Simberloff 2011; Simberloff *et al*. 2013; Hixon *et al*. 2016; Nentwig *et al*. 2016; Sutherland *et al*. 2016; Hulme 2017; Ricciardi *et al*. 2017). A source of contention often appears over whether a species is detrimental or advantageous depending on which societal perspective is taken and the manner in which the invasion is mediated (Schlaepfer *et al*. 2012; Schwartz *et al*. 2012; Simberloff *et al*. 2013). There are many cases of species being redistributed outside of their native range, however, not all become invasive due to not being capable of surviving and reproducing within the new environment (Mack *et al*. 2000). Equally, some non-indigenous species can provide ecosystem services and even replace native resources (Elgersma & Ehrenfeld 2011; Pattemore & Wilcove 2011). Some damaging species are introduced intentionally for biocontrol, such as the cane toad in Australia (see Urban *et al*. 2007) or for aesthetic (Nuñez & Simberloff, 2005) or sports purposes (Courtenay 1997). These populations are cultivated on purpose, which allows them to reach a size that is too high to control (Mack *et al*. 2000). The mathematics of an invasion have been compared to the persistence of disease or parasites, such that there is a threshold population size, a characteristic population growth and various environmental mitigating effects on the success of an alien species becoming naturalised (Mack *et al*. 2000).

Invasiveness can be explained through an analysis of specific traits in the invader and the occurrence of favourable ecological and genetic factors (Colautti *et al*. 2014). Relocation of species can remove environmental pressures found in their native range, such as enemy release, prey naïveté and abiotic factors, consequently there are few exacerbating factors that halt their progress (Elton 1958; Mack *et al*. 2000; Anton *et al*. 2016). Additionally, this absence positively affects fitness but also increases prospects for growth and longevity (Caño *et al*. 2008). Ricciardi and Cohen (2006) attempted to quantify 'invasiveness' by accounting for the rate of species establishment and rate of spread combined with the already documented effects on native species. By combining occurrence data (or survival and reproductive data) with a quantification of 'impact' a descriptive and powerful prediction tool can be created (Dick *et al*. 2013; Dick *et al*. 2017a,b; Laverty *et al*. 2017b).

Biological invasions are happening at an increasing rate due to developing connectivity and climate change increasing species ranges (Mack *et al*. 2000; Margolis *et al*. 2005; Pimentel *et al*. 2004; Wonham and Carlton 2005; Mellin *et al*. 2016; Rouget *et al*. 2011; Hulme 2017). Invasions do not have borders, therefore are a global concern (Mack *et al*. 2000; Pimentel *et al*. 2004), especially within the marine environment. Due to the interconnected nature of the marine environment range expansion and invasions may be considered as less troublesome when compared to terrestrial island invaders (Simberloff 1995), however, this could be related to a study bias. Man-made structures such as the Suez Canal allow enhanced migrant flow from the Red Sea to the Mediterranean (Por 1978) and vice versa (Galil *et al*. 2016). Alien species can cause economical loss and threaten already endangered species as well as causing a general reduction of biodiversity (Pimentel *et al*. 2004). Invasions bring with them many new species interactions that lead to displacement of native populations such as: direct predation (Fritts & Rodda 1998; Preston *et al*. 2012); transfer of disease (Prenter *et al* 2004; Hershberger *et al*. 2010); hybridization (Mooney & Cleland 2001; Luquet *et al*. 2011); novel community assemblages (Walther 2010; Ordonez 2016) and interspecific competition for resources (Brown *et al* 2002; Raymond *et al*. 2015).

The largemouth bass (*Micropterus salmoides)* has been called one of the World's Worst Invaders (Lowe *et al*. 2000) in freshwater systems; the success of the species appears to coincide with the simplification and exploitation of habitat (Alexander *et al*. 2015). The largemouth bass was introduced in South Africa as a sport fish and it has been shown to negatively affect native prey communities (Yonekura *et al*. 2004) through a top-down cascade, which further causes a reorganization of food webs and interactions due to a change in predator pressure (Zaret & Paine 1973; Maezono *et al*. 2005). The overexploitation of haplochromines facilitated the invasion of Nile perch (*Lates niloticus)* in Lake Victoria. This invasion caused the further extinction of many species of haplochromine (Witte *et al*. 1992) and consequent phase shift to allow increased shrimp recruitment leading to an ecosystem dominated by four main species (Goudswaard *et al*. 2008; Downing *et al*. 2012). Rainbow trout (*Oncorhynchus mykiss)* interrupt resource flow in forest stream systems and drive community shifts within the native populations and habitat through usurping the flow of insects falling into the stream, causing native comparators to prey switch leading to a phase shift to excess algae in the stream

(Baxter *et al*. 2004). It has been noticed that after an invasion, species possess the ability to evolve to suit their new ranges (Mack *et al*. 2000), for example, the macroalgae *Caulerpa taxifolia* developed a new thermal tolerance to allow it to survive in the colder Mediterranean (Phillips & Price 2002). In these incidences, an invasive species changed the interactions within a healthy and functioning ecosystem and caused loss to biodiversity and economy because there was not an expected consequence of the invasion or the invasion itself was unforeseen. Therefore, there was a lack of understanding regarding how the alien species were successful and what traits are attributed to this. By combining knowledge of the 'invasiveness' of a species, such as reproductive traits, with the *per capita* impact of an individual it would be possible to develop a comprehensive impact prediction metric such as in Dick *et al*. (2017b) (see Chapter 6). This is a metric that can be applied across the board taxonomically and assess both traits of 'invasiveness' and 'impact' in terms of measurable changes in prey populations. By utilising such methods there is great potential in creating impact predictions under numerous circumstances, including invasions and climate change. The method proposed is examined closer below (see 1.3) and in Chapter 6.

It is becoming increasingly clear that the synergy between climate change and invasive species is more important, with regards to ecological and socio-economic concerns, than their effects on global change as individual drivers (Shine *et al*. 2010; Smith *et al*. 2012; Ricciardi *et al*. 2017). It is difficult to predict precisely how species will respond to climate change due to the number of life stages, however, change will undoubtedly occur and community structure will be altered (Hsieh *et al*. 2009; Field *et al*. 2010; Doney *et al*. 2012). As mentioned before, the interconnected nature of marine environments facilitates an accelerated rate of ecological change and natural range expansion within the system (Stachowicz *et al*. 2002; Occhipinti-Ambrogi 2007 Côté & Green 2012). There is dispute over the terminology and definitions of invasive species (Warren 2016; Russell & Blackburn 2017;) and this should be considered further, that with climate facilitated change, the definition of invasive species may also change (Valéry *et al*. 2008). Previously an ecological invasion is defined as being mediated by human translocation, however, in the future native species may develop changing traits that could be aligned to invader effects (Valéry *et al*. 2008; Carey *et al*. 2012), this is investigated in Chapters 3, 5 and 6. These include increased propagule pressure, increased

development time, and increased *per capita* response (Pörtner *et al*. 2001; Ward & Masters 2007; Johnston *et al*. 2009; Laverty *et al*. 2017b).

Species distributions are determined often through physiological thresholds such as temperature, oxygen concentration and pH (Hansen 2002, Drinkwater 2005, Guinotte & Fabry 2008). These abiotic factors determine resource abundance, how the consumer interacts with the resource, and regulate organism physiology (Hughes *et al*. 2003; Harley *et al*. 2006; Buisson *et al*. 2008; Monaco & Helmuth 2011). Climate envelopes, under a scenario of general warming, will shift pole-ward (Perry *et al*. 2005). Range shifts in species are well documented (Newson *et al*. 2009; Auber *et al*. 2015), however, inter-annual variability can make it difficult to discern trends (Morin & Thuiller 2009). Furthermore, sedentary species that cannot move with the climate envelope will be subject to a series of extirpation events (Walther *et al*. 2002). Climate regimes may dictate invasive species impacts (Hellmann *et al*. 2008; Rahel & Olden 2008; Walther *et al*. 2009), as such the climate determines their abundance, their range and potential *per capita* effects (Parker *et al*. 1999; Walther *et al*. 2009). Temperature is an important factor when regarding climate change, particularly as it has direct and indirect effects on all biological processes and across a range of scales, from molecular to behavioural (Pörtner *et al*. 2006). Under predicted scenarios, and indeed already, non-native species from adjacent areas can cross what were previously physiological boundaries and become new elements of biota (Garcia Molinos *et al*. 2016).

The invasiveness of a species can be mediated by abiotic factors as demonstrated by MacNeil *et al.* (2004) (oxygen concentration); Alcaraz *et al.* (2008) (salinity); Kestrup and Ricciardi (2009) (conductivity). As the habitat they occupy shifts away from its optimal, the impact of said invader declines (Iacarella *et al*. 2015). Therefore, the establishment of a species relies upon the new ecological parameters within its invaded range and the trade-off between the species-specific physiology and the ecological constraints of the novel environment (i.e. resource abundance, predatory pressure) (Peck *et al*. 2009).

Marine invasions are very difficult to stop once they have become established, due to the high connectivity between vast oceanic systems caused by complex currents and oceanographic features (Drake & Lodge 2006), combined with shipping and trade routes acting as distribution vehicles via ballast water. Invasive species have resulted in the endangering of many species (Pimentel *et al*. 2004;

Tilman *et al*. 2017), thus it is essential that a predictor is developed to identify future invaders and the damage that they may cause if it is going to be possible to mitigate further invasion effects (Mack *et al*. 2000; Dick *et al*. 2014; Laverty *et al*. 2017b) (Chapter 2). By combining current invasive species impact prediction methods (Dick *et al*. 2014; Dick *et al*. 2017a,b; Laverty *et al*. 2017b) with knowledge of predicted abiotic factors, factorial experiments can be conducted in which it will be possible to elucidate *per capita* effects and impact potential under a series of scenarios for both predicted invaders and native species (Chapters 2, 3, 5, 6). An issue arises due to the concept of short term laboratory experiments not allowing for long enough acclimation times, and this then introducing bias through inducing stress in the organisms. Peck *et al*. (2009) addressed precisely this problem, as laboratory experiments generally do not realistically represent the rate of warming, thus they investigated how the rate of warming affects individual and species survival. It was ascertained that when temperatures were raised by 1°C per day, there was much lower survival rates than when temperatures were raised slowly and on a scale of weeks or months. While aquaria based experiments are useful to investigate the mechanistic details of thermal tolerance, they are not representative of natural situations and do not account for site specific microclimates that occur in the wild (Peck *et al*. 2009). This is discussed further, in context of the experiments in Chapters 3 and 5.

1.3 Functional Response (FR) and Relative Impact Potential (RIP) as new methods in predictive invasion ecology

1.3.1 FR phenomenon and experimental design

The Functional Response (FR) is a classical ecological phenomenon that describes the rate of resource consumption with regards to resource density (Solomon 1949; Holling 1959, 1965, 1966). Solomon (1949) and Holling (1959) described three response curves, wherein Type I is a linear response wherein handling time is not limited by the resource density (MacNeil *et al*. 1997; Jeschke *et al*. 2004) (See Fig. 1.1). Type II functional responses are characterized by a decelerating intake rate where the consumer is limited by behavioural and/or physiological processes, with such responses potentially leading to prey extirpation due to high proportional predation at low prey densities (Juliano 2001) (See Fig. 1.1). Type III functional responses are sigmoidal, with low proportional intake rates at low

prey densities (Holling 1959) and thus lead to low prey density refugia and can potentially stabilise prey populations (See Fig. 1.1). Holling (1959) created the original mathematical description of the Type II functional response, known as Holling's disc equation. However, the mathematical function for Type III responses was somewhat convoluted, so was simplified by Real (1977) using an analogy of allosteric enzymes and the Michaelis-Menton model. Type III responses have typically been associated with predator learning (Dawkins 1971; Krebs 1974; Real 1977) and prey switching behaviours (Akre & Johnson 1979). There is some debate around the idea that Type III responses can and do occur in single predator – prey environments as there is no need for switching behaviours to occur (Murdoch *et al*. 1975; Kalinkat *et al*. 2011).

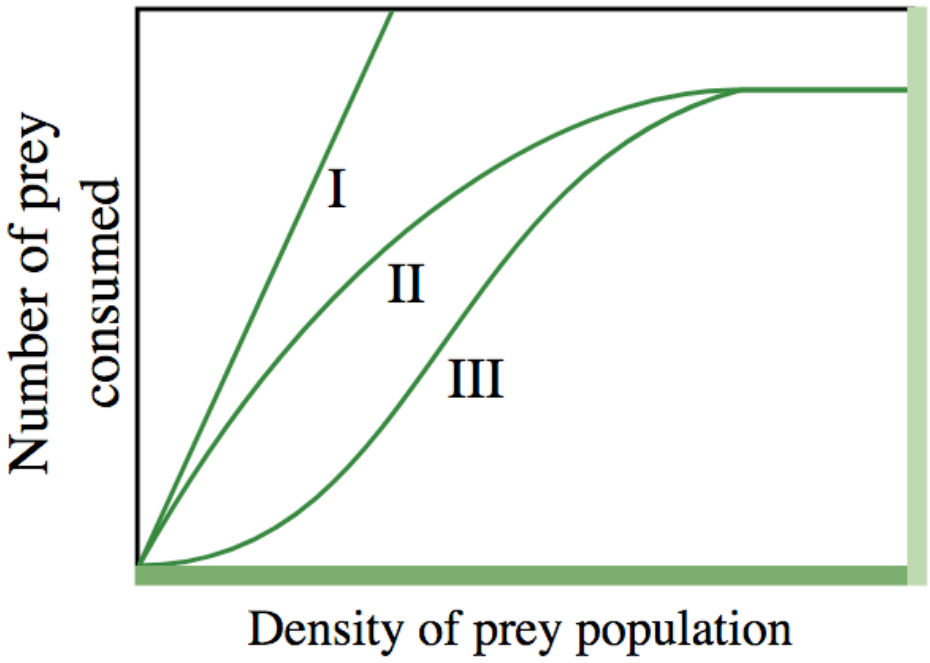

Fig. 1.1 Graphs showing categorical functional response types (Type I, Type II, Type III)

One of the main developments of functional response analysis is getting the most accurate parameter estimates as these are the mechanistic components of the functional response. The parameters are attack rate (*a*), handling time (*h*) and maximum feeding rate estimate, the latter defined as 1/*h*T, wherein T is a constant fixed at 1 that represents the total time available for predation (Houck & Strauss 1985). Therefore, handling time is estimated as a fraction of T, and in this case, represents several behaviours related to the searching, subduing, processing and digestion of prey items (Jeschke *et al*. 2002). Attack rate is defined as the rate of potential detection and is expressed as a function of the number of encounters (Real 1977). To get the parameter estimates, the disc equation must be solved, but the disc equation relates explicitly to a predator searching at a constant speed for randomly distributed prey items at a constant handling time, with a constant prey density (Holling 1959; Houck & Strauss 1985). This becomes a logistical issue when trying to experimentally derive values for the functional response of a species due to having to replace prey as they are consumed. This lead to the development of the Random Predator Equation derived by both Rogers (1972) and Royama (1971) which incorporates prey depletion into the model.

The Random Predator Equation becomes difficult to analyse due to the appearance of one of the predictor values (N_e : the number of prey consumed) on both sides of the equation (Livdahl & Stiven 1983; Houck & Strauss 1985), therefore, Juliano & Williams (1985) recommended the use of non-parametric parameter space and non-linear regressions with standard deviations and 95% confidence intervals when comparing between curves. Further, the Random Predator Equation can give unreliable parameter estimates when there is a high degree of individual animal variation in consumption (Houck & Strauss 1985).

Experimental design must be sufficiently optimised to account for variation and accurate parameter estimates, while being ecologically relevant (Dick *et al*. 2014). This involves use of a design incorporating replicated feeding trials wherein: the total time available is kept constant; the predator is always subject to the same pre- and -post trial conditions; individuals body sizes must be relatively similar and there must be several prey densities investigated to allow variability of response to be incorporated into the results (Houck & Strauss 1985). After trials the results can be collected as a binomial distribution of numbers wherein the number of prey consumed versus the number of prey not consumed can be used to assign weights

and then used to estimate maximum likelihood (Houck & Strauss 1985). Houck & Strauss (1985) advocate various statistics to test for differences between functional response curves, these include use of the F test derived from a general linear model, and non-parametric rank sum tests such as Mann-Whitney Wilcoxon test.

Further development of the methodology has led to enhancement of the comparison of responses and the parameters within. These are outlined in Pritchard *et al*. (2017) using the 'frair' R package (R Development Core Team 2016; Pritchard *et al*. 2014). As it stands, there are two schools of comparison; the first involves modelling the functional response by implementing the Lambert W function (Lambert 1758), and from there bootstrapping the parameters (n=2000) to generate clouds of 95% confidence intervals around the response curve. This allows direct visual comparison of the functional response and relates to populations rather than within samples, as such overlapping of the bootstrapped clouds indicates no significant difference between the curves (Barrios-O'Neill *et al*. 2014). Others prefer to bootstrap the parameters (e.g. n=30) and then compare non-parametrically between them using generalized linear models with a quasi-Poisson distribution (Alexander *et al*. 2015; Laverty *et al*. 2015). There is a function within 'frair' (Pritchard *et al*. 2014) that allows direct comparison between functional response parameters using a z test (Juliano 2001), however, this is only applicable when the Type of response is the same and the starting parameters are the same, this is consequently limited. This leads to discussion between using categorical Type I, Type II, Type III models or using a flexible model to avoid the uncertainty of categorical models (Real 1977; Kalinkat *et al*. 2013; Barrios-O'Neill *et al*. 2014). The flexible model uses a scaling exponent (q) which can be fixed at 1 or 0 or intermediately at 0.5, as q becomes >0 it becomes more sigmoidal and approaches a Type III response (q=1) (Real 1977; Vucic-Pestic *et al*. 2010). The merits of each method will be explored and assessed in this thesis but the comparative approach will be the main focus as it is more phenomenological than mechanistic.

1.3.2 Analysis

The analyses in this thesis were carried out in accordance with the methods listed below. Functional response Type (I, II, III) was determined using a logistic regression of the proportion of prey consumed against prey density. If the proportion

of prey consumed decreases with increasing prey density, then the logistic regression will produce a significantly negative first order term and thus the functional response Type will be classed as Type II (Juliano, 2001). If the logistic regression produced a non-significant first order term, a generalised linear model (GLM) was run on the proportional data, in this case a Type II response would be signified by a significantly negative first order term followed by a significantly positive second order term (Juliano, 2001), while a Type III is signified by a significantly positive first order term and significantly negative second order term (Juliano, 2001). A Type I functional response could be determined from a non-significant first or second order term, however a Type I is categorical only in filter feeders or systems that meet the requirements stated in Jeschke *et al*. (2004). Therefore, when non-significant terms are encountered, a scatterplot with locally weighted scatterplot smoothing (LOWESS) lines were fitted to assess the direction of proportional consumption by using a 9/10 smoothing factor fitted to the data of number of prey eaten out of the number of prey supplied.

1.3.2.1 Prey non-replacement analysis

When a Type II response was indicated as above, the functional responses were modeled using Rogers' (1972) Random Predator Equation (Equation 1.1), due to the prey density being depleted (Juliano, 2001):

$$N_e = N_o\left(1 - exp\big(a(N_e h - T)\big)\right) \qquad \textbf{Equation 1.1}$$

N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h is the handling time and T is the total time available. The Lambert W function was applied to fit the model to the data (Bolker, 2008).

In the instance of Type III functional responses, Hassell's Type III response (Equation 1.2) was modeled to the data wherein a is a hyperbolic function of N_o (Juliano 2001), where b, c and d are constants and prey are depleted:

$$N_e = N_o\{1\text{-}exp[(d + bN_o)(hN_e\text{-}T)/(1 + cN_o)]\} \qquad \textbf{Equation 1.2}$$

Flexible models were also used on the data (Equation 1.3). Categorical Type

II functional responses are $q = 0$ and, when $q > 0$, the functional response becomes proportionally more sigmoid and $q = 1$ indicates a Type III response. Treatments with GLMs indicating Type III were also modeled with a flexible model with q fixed at 1, Type II were modeled with q fixed at 0, additionally q was fixed at 0.5 to determine whether an intermediate response was more parsimonious with the data. The flexible model is a variation of Rogers' Random Predator Equation (Equation 1.1) with the addition of a scaling exponent q (Real 1977; Vucic-Pestic *et al*. 2010).

$$N_e = N_0 \left(1\text{-}exp\left(bN_o^q(hN_e\text{-}T)\right)\right) \qquad \textbf{Equation 1.3}$$

Where N_e is the number of prey consumed, N_o is the initial prey density, b is the search coefficient, h is handling time, q is the scaling coefficient, and T is the total time available. The search coefficient in Equation 1.3, b combines with N_o and q to produce attack rates that vary with prey density, (i.e. $a = bN_o^q$) as opposed to Equation 1.1 where attack rate is fixed at all prey densities (N_o).

1.3.2.2 Prey replacement analysis

The replacement model works under the assumptions of Holling's disc equation (Equation 1.4) (Holling 1959) when a Type II functional response is indicated (Juliano 2001):

$$N_e = (aNT)/(1 + aNh) \qquad \textbf{Equation 1.4}$$

Whereupon N_e is the number of prey consumed, N is the density of prey supplied, a is the attack constant, h is the handling constant and T is the total time available. From this, the estimated maximum feeding rate can be calculated as $1/hT$ as estimates for h are delivered from the model. Type II functional response assumes that attack and handling parameters remain constant across all prey densities, however, when considering Type III responses, a becomes a function of prey density, and therefore a is a hyperbolic function of N_o (Juliano 2001).

Flexible models were modelled for the replacement data when non-significant logistic regression and GLM terms were encountered (Equation 1.5). These assume prey replacement and implement the same relationships as in Equation

1.3, wherein when $q > 0$ the response becomes progressively more Type III. When $q = 0$, $a = b$ and the relationship becomes the same as Equation 1.4.

$$N_e = (aN_oT)/(1 + aN_oh) \quad \textbf{Equation 1.5}$$

Where N_e is the number of prey consumed, N_o is the initial prey density, b is the search coefficient, h is handling time, q is the scaling coefficient, and T is the total time available. The search coefficient in Equation 1.5, b combines with N_o and q to produce attack rates that vary with prey density, (i.e. $a = bN_o^q$).

1.3.3 Relative Impact Potential

The use of comparative FRs has been utilised further by altering the Parker-Lonsdale equation (Parker *et al*. 1999) wherein Impact (I) of a species can be quantified by Range (R), Abundance (A) and *per capita* effect (E) (Equation 1.6).

$$I = R \times AB \times E \quad \textbf{Equation 1.6}$$

Dick *et al*. (2017b) developed an Impact Potential (IP) metric which removes the range and makes IP the product of abundance (AB) and FR as a proxy for the *per capita* effect of a consumer (Equation 1.7).

$$IP = AB \times FR \quad \textbf{Equation 1.7}$$

From this Dick *et al*. (2017b) propose a Relative Impact Potential (RIP) which compares the impact of an invader to that of a native (Equation 1.8). Where the RIP is <1 the invader will have less impact than the native predator, when RIP = 1 the invader will have no impact above the native predator, and where RIP >1 there will be likely invader impact on prey populations. The method outlined can also incorporate uncertainty into the prediction by use of standard deviations and confidence intervals (Dick *et al*. 2017b; Laverty *et al*. 2017b). From this the goal is to determine a probability density function (pdf) for the RIP measure through use of means and standard deviations which is used to conclude the probability of the RIP measure being greater than 1. Here Equation 1.8 is modified to become Equation 1.9,

wherein $f()$ indicates the pdf. The merit, use and development of these equations is covered in Chapter 6.

$$\text{RIP} = \left(\frac{\text{FR invader}}{\text{FR native}}\right) \text{x} \left(\frac{\text{AB invader}}{\text{AB native}}\right) \qquad \textbf{Equation 1.8}$$

$$f(\text{RIP}) = \left(\frac{f(\text{FR invader})}{f(\text{FR native})}\right) \text{x} \left(\frac{f(\text{AB invader})}{f(\text{AB native})}\right) \qquad \textbf{Equation 1.9}$$

Predicting the ecological consequences of invasions, both terrestrial and aquatic, is a huge challenge and objective of fundamental importance to ecologists, conservations and managers alike (Mack *et al*. 2000; Ricciardi 2003; Dick *et al*. 2013; Simberloff *et al*. 2013; Caffrey *et al*. 2014; Dick *et al*. 2014). Mack *et al*. (2000) note that previous efforts to ascertain general success traits of invasive species has proved to be inconclusive, therefore it is a growing priority to be able to identify and assess the damage caused by emerging and recent invasions, rather than just retrospectively as it has often been (Ricciardi 2003). Morrison and Hay (2011) propose that the most damaging invaders are those that most efficiently deplete native resources, this is supported by Dick *et al.* (2013) and Simberloff (2009) where it is suggested that a successful invader is closely linked to the rapid utilisation of resources. Comparative FR analysis has thus been pioneered as a way of assessing invasive species impacts, where the maximum feeding rate and FR Type become a quantification of interaction strength and thus a proxy for ecological impact (Dick *et al*. 2013; Dick *et al*. 2014; Barrios-O'Neill *et al*. 2014; Alexander *et al*. 2015; Dick *et al*. 2017a,b; Laverty *et al*. 2017b). Wherein FR represents ecological impact, which is defined as a measurable change of the state of an (invaded) ecosystem (Ricciardi *et al*. 2013). It serves to give both a mechanistic and phenomenological understanding of predation dynamics within a specific predator-prey system under specific abiotic parameters (Dick *et al*. 2014; Barrios-O'Neill *et al*. 2014; Alexander *et al*. 2015; Dick *et al*. 2017a,b; Laverty *et al*. 2017a,b). As such, the derivation and comparison of functional responses combines mechanistic modelling with empirical data to be a robust and resilient test of impact (Dick *et al*. 2013; Dick *et al*. 2014; Dick *et al*. 2017a,b; Laverty *et al*. 2017a,b).

There has been emphasis on understanding the contextual variation of functional response manifestation, such that the predatory response to varying prey

densities is altered by suites of abiotic factors in addition to the basic form of the response (Real 1977; Real 1979). Alexander *et al*. (2015) investigated this and observed that the kill rate of an invader increased in simplified habitats, while the functional response remained Type II. Increased temperature and parasitic load increased the magnitude of the functional response and therefore the impact of an invader (Laverty *et al*. 2017a). This demonstrated the contextual dependencies of the functional response but also showed synergy between two factors enhancing the response. Furthermore, this use of functional response analyses allows insight into the consequences for native populations of resources due to the invasion and which species could be further affected by the top-down cascades that invasive species often instigate (Nyström *et al*. 2012; Campbell *et al*. 2013; Dick *et al*. 2017a,b). The combination of abundance and FR in the RIP metric can be further improved upon by investigating different contexts and their potential synergies to give a complex picture and highlight at risk prey populations and locations, and high-risk scenarios (Chapter 6).

Functional response experiments are ordinarily completed in a laboratory setting, following the recommendations described above. These experiments are informative but often are somewhat simplistic in the environments delivered and do not usually mimic the natural movement of prey between patches. These issues can be resolved by complimenting laboratory studies with field data (such as Smout & Linstrøm 2007; Dick *et al*. 2013; Barrios-O'Neill *et al*. 2014) in order to further inform and corroborate predictions (Chapter 4). It is also possible to observe functional responses in sitú which is more practical for larger species and species with complex needs. Hines *et al*. (1997) carried out functional response work based upon observation of feeding events in eagle rays (*Myliobatis tenuicaudatus*), whereas Middlemas *et al*. (2006) did a study based upon reconstructing the diet of harbour seals (*Phoca vitulina*) through scat compositions and prey abundance surveys. Documenting functional responses *in situ* can be misleading as predators are expected to aggregate in patches where prey is abundant thus making it difficult to successfully document feeding rates in less abundant patches (Beauchamp 2009).

A merit of functional response analysis is that it can be used to investigate ecological impact under numerous contextual influences, and combined with relevant field data on abundance or fecundity it could be subverted from being a predictor of biotic invasions to a general predictor of relative ecological impact by native species

under climate change scenarios (Real 1979; Laverty *et al*. 2015; Dick *et al*. 2017a,b). This is in line with the assertion that native species may become invaders or akin to invaders under new abiotic regimes (Valéry *et al*. 2008; Carey *et al*. 2012). This is investigated further in this thesis where the functional response of native predator species is assessed under predicted future temperatures in order to understand how temperature change could affect economically important species. In Chapter 6 the RIP metric is developed in order to show how species impact can change under climatic variation and how this metric can inform policy management to ensure sustainability in the future.

1.4 Northern Irish Fisheries

The Irish Sea (ICES area VIIa) comprises an area spanning around 58000km^2 between the British Isles and Ireland, joined to the Celtic Sea in the south by St George's Channel (Vincent *et al*. 2004). It is a comparatively shallow area with substrate comprising of mainly sand and gravel (Parker-Humphries 2004). There is considerable connectivity between the Irish Sea and the North Atlantic, thus making the area highly susceptible to large-scale regime changes occurring in the North Atlantic (Parsons & Lear 2001; Marshall *et al*. 2001; Lees & Mackinson 2007). The movement of water within the Irish Sea flows north to south and is dominated by an anti-clockwise gyre, which regulates circulation (Lees & Mackinson 2007). The temperature range lies around 6°C in winter to maxima of 16°C in summer (Lees & Mackinson 2007).

Commercial fisheries are integral to rural life as a source of economy and food security, but also as part of a traditional basis of life (Richardson 2016). Northern Irish (NI) fisheries consist of numerous shellfish, pelagic and demersal species, and the most important by value, of each class being *Nephrops norvegicus,* herring and mackerel, and monkfish and anglerfish respectively (Richardson 2016). The *Nephrops* fishery is the most productive NI fishery, and is fished exclusively by 82% of the NI fleet and brings in around £80m at first sale (Richardson 2016). It is thought that the Irish Sea area has an annual economic contribution of £6bn (Vincent *et al*. 2004). In 2015 16000 tonnes of dogfish were landed, at the value of £0.3m, nonetheless, populations of lesser spotted dogfish (*Scyliorhinus canicula,* hereafter referred to as dogfish) and nursehounds (*Sycliorhinus stellaris*) are stable and

increasing within the Irish Sea (Richardson 2016). The European Commission has declared mackerel, cod and whiting fisheries out of safe biological limits within the Irish Sea in 2012 (Richardson 2016). Consequently, there has been an increased emphasis from the European Commission and the Northern Ireland Assembly in providing funding and support for projects that can make the industry more sustainable and projects that provide the basis for policy and decision making.

In Northern Ireland, there is a predicted average temperature rise of 3°C or more across the coming century (2080) and a SST rise by 2.5°C (Hulme *et al*. 2002). This may drive changes in species distribution and composition, increases in invasive species and their ranges (Anderson *et al*. 2005; Berry *et al*. 2005), and threats to inter-tidal habitats due to flooding and erosion (Harrison *et al*. 2001; West & Gawith *et al*. 2005). However, temperature rises may benefit aquaculture due to higher growth rates and opportunities for new species (See table 3.2 Hulme *et al*. 2002). With an ever-expanding human population there are growing concerns about food security (Godfray *et al*. 2010; Godfray *et al*. 2011). Marine species have been a traditional food source for many countries and currently provide around 50% of animal protein to 400 million people (FAO, 2011). According to UN-WHO (2002), the highest rate of human growth occurs in areas where fish are the main source of non-grain protein, thus it is imperative that the sustainability of fisheries is maintained to provide essential nutrition, but whether this will happen depends upon the precise nature of climatic changes and the management of specific fisheries (Worm *et al*. 2009; Costello *et al*. 2012).

There must be site-specific management and adaptive policies to ensure the continued sustainability of Northern Ireland sea fisheries and aquaculture (ASC 2016). This can be achieved through development of accessible tools that inform stakeholders and policy makers of the possible outcomes of climate forced change (Stokes *et al*. 2006; ASC 2017). By delivering informative risk assessments that are pre-emptive and match the priorities and needs of stakeholders while incorporating the associated uncertainties it will allow the implementation of adaptive strategies in management of resources such as changes to total allowable catch (TAC) and quota allocations (Stokes *et al*. 2006; SNIFFER 2007; ASC 2016). This is increasingly important as, according to the IPCC Mitigation Report (Edenhofer *et al*. 2014), rural areas i.e. the majority of Northern Ireland fishing communities, will be disproportionately affected by the impacts of climate change. An increased

development of aquaculture practices is a way forward that has been identified by multiple sources (Cohrane 2009; Garcia and Rosenberg 2010; Rice and Garcia 2011; Merino *et al*. 2012), as these species are predicted to benefit from increased temperatures. Investments need to be made to reduce the uneven skew of aquaculture production as Asia currently dominates the world's production of aquaculture products (FAO 2012). ASC (2016) highlighted the urgent need for further research on the effect of climate change on marine fishery resources so as to be able to make well informed policy decisions and adaptation measures to assure economic and ecological stability.

With these priority needs in mind this thesis investigates the development of an accessible metric (Chapter 6) to inform stakeholders and policy makers of the implications of changing environmental factors on the ecology of important marine species. It demonstrates how a cohesion of well-informed experimental practices (Chapters 2, 3, 5) and field surveys (Chapter 4) can be used to assess the way the ecological impact of a species may change and possibly have implications for the sustainability of important fisheries and the economies that rely on them. This will supply the evidence needed for policy makers to act upon to reduce pressure from existing sources in order to maintain resource sustainability.

1.5 Objectives

It is clear how future changes in climate may present themselves, but there remain unknowns in the effects of these climatic variables upon biotic interactions (Gilman *et al*. 2010; Dawson *et al*. 2011). These are key drivers of structure (Beaugrand *et al*. 2002; Genner *et al* 2004; Wernberg *et al*. 2016) and function (Holmlund & Hammer 1999; Selim *et al*. 2016) of biotic assemblages. The challenges lie in picking apart the nuances of these interactions as they are mediated by many complex mechanisms driven by both predator and prey species. Furthermore, they are further complicated through the existence of trophic cascades (Sanford 1999; Menge 2000) and feedback loops, which cause species specific predictions to be confounded (Suttle *et al*. 2007; Tylianakis *et al*. 2007; Williams *et al*. 2008; Baum & Worm 2009). While many studies have focused on the prediction of range expansion (Thomas *et al*. 2004; Graham *et al*. 2006; Reugg *et al*. 2006), invasion facilitation (Stachowicz *et al*. 2002; Kelley 2014), and single species physiological effects (see meta-analysis in Rosenblatt & Schmitz 2014) of climatic

change, few have conducted empirical, mechanistic studies which investigate context dependent biotic interactions. This is due to the many confounds within such a study and the practicality of the experiments themselves. Many studies have investigated the response of tropical species (Ferrari *et al*. 2014; Miller *et al*. 2015) and species adapted to extreme cold (Pörtner 2006) to changing abiotic values due to the ecological relevance of temperature adaptation. Therefore, the effect of temperature on temperate species is somewhat understudied. It is hypothesised that due to the range of temperatures that species in higher latitudes are exposed to, that they will be less vulnerable to climatic change (Janzen 1967; Sunday *et al*. 2011). In comparison, species that are adapted to areas with stable and more defined temperature ranges such as the tropics and poles, will be more susceptible to slight perturbations (Janzen 1967; Sunday *et al*. 2011). Nonetheless, there are few empirical examples that can support this hypothesis; especially ones that investigate the responses of large bodied vertebrates and intertidal vertebrates. This is an oversight with regards to creating feasible and accurate management policies as they cannot be properly informed without considering effects of both predator and prey population dynamics. Thus, without the use of mechanistic and phenomenological models to assess and predict the causative drivers of population change fisheries management is lacking key information (Malanson *et al*. 1992; Ochipinti-Ambrogi 2007; Gilman *et al*. 2010; Dawson *et al*. 2011).

The aim of this thesis is to identify how temperature will affect ecologically and economically relevant Irish Sea predator-prey interactions with regards to prey density, abiotic context and species specificity, and to predict the impact of predator-prey interactions of a successful invasive species (lionfish; *Pterois volitans*) under different abiotic contexts. In the second chapter I characterise the functional response of lionfish under a number of abiotic scenarios. Marine teleost invaders are somewhat rare and this makes a poignant case study to understand and predict the impact of other potential invaders facilitated by climate change. Further, while the chances that a lionfish invasion will occur in UK waters is low, there are signs of invasion in the Mediterranean (Turan *et al*. 2014; Oray *et al*. 2015; Kletou *et al*. 2016; Azzuro *et al*. 2017), therefore pre-emptive work is required. In the third chapter I investigate the differences between prey supply models and three raised temperatures on the parameters of the functional response of the bleniid *Lipophrys pholis* (shanny). I attempt to understand how a temperature gradient will affect the

consumption of prey in an intertidal teleost predator. In the fourth chapter I describe the current diets of a commercial predator, (cod; *Gadhus morhua*) and a non-commercial predator (dogfish), with regards to dietary overlap and substrate type. In the fifth chapter I use a two by two experimental design to understand how acclimation to raised temperature differentially affect dogfish functional responses to prey (*Echinogammarus marinus*). In the sixth chapter I utilise a new invasion impact prediction method, Relative Impact Potential (RIP; Dick *et al*. 2017b; Laverty *et al*. 2017b) to create a metric and user-friendly output for predicting climate change impacts on prey populations.

Chapter 2

Predatory impact of the invasive lionfish (Pterois volitans): effects of temperature, habitat complexity and light on the functional response

The data collected from this chapter arise partly from J. South's undergraduate dissertation, M. McCard's undergraduate dissertation project supervised by J. South, and A. Anton's joint project with J. South. All data analysis and report writing was carried out by J. South.

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2.1 Introduction

Invasive species are a global cause for concern due to their detrimental impacts on both the economy and biodiversity (Mack *et al.* 2000; Pimentel *et al.* 2004; Simberloff 2011; Dick *et al*. 2013; Simberloff *et al.* 2013; Dick *et al*. 2014). Therefore, there is currently an emphasis on developing predictive methodologies that allow robust forecasting of invasion impacts (Dick *et al.* 2013; Simberloff *et al.* 2013; Caffrey *et al.* 2014; Dick *et al*. 2014). Many hypotheses and impact prediction methodologies are not pre-emptive and do not take abiotic and biotic context dependency into account (Pimm 1989; Ricciardi 2003; Kulhanek *et al.* 2011). This is problematic as invasions often take place across a range of contexts which interact to determine behaviour and therefore invasiveness and impact (Laverty *et al*. 2015; Paterson *et al.* 2015).

Functional response analysis has been successful in invader impact prediction across numerous trophic groups and taxa and, furthermore, current research shows its merit in predicting impact under different abiotic and biotic contexts (Laverty *et al.* 2015; Alexander *et al.* 2015). These methods give a unified quantification of predatory impact under multiple abiotic and biotic contexts, thus delivering a robust impact prediction technique (Dick *et al.* 2014; Paterson *et al.* 2015).

The lionfish (*Pterois volitans* and *Pterois miles*) invasion in the Caribbean and Gulf of Mexico was first reported in 1985, and more recently the presence of *P. miles* has been documented in the Mediterranean (Turan *et al*. 2014; Oray *et al*. 2015; Kletou *et al*. 2016; Azzuro *et al*. 2017). The success of this invasive marine teleost has prompted many studies on its behaviour and effects of the invasion (Kimball *et al.* 2004; Schofield 2010; Albins & Hixon 2011; Biggs & Olden 2011; Côté *et al.* 2014; Anton *et al*. 2016). These studies have highlighted the generalist nature of lionfish predatory feeding, indiscriminate habitat selection and diversion from their crepuscular feeding strategies (Côté & Maljković 2010). The Caribbean and Gulf of Mexico and the Mediterranean are vulnerable systems, at risk due to anthropogenic and climate change factors (Jackson *et al.* 2001; Pandolfi *et al.* 2003), therefore the lionfish invasion poses considerable threat, not only to the biodiversity of the area but to the local fishing industries (Albins & Hixon 2013). It is thus important to investigate how resource consumption of lionfish varies within the

context of current and future abiotic parameters (Englund *et al.* 2011; Dick *et al.* 2014).

Climate change effects include rise in temperature, which may facilitate range changes through thermal acclimation. Temperature also regulates physiology, thus increasing metabolic costs (King 2005; Pörtner & Knust 2007; Gilbert *et al.* 2014). Furthermore, temperature increase causes degradation of coral reef complexity (Alvarez-Filip *et al.* 2009). Habitat complexity and presence of refuge is a mediator of predation strength and therefore a driver of community structure (McCoy & Bell 1991; Hatcher 1997; Warfe *et al.* 2008; Graham 2014; Rogers *et al.* 2014). Lionfish abundance is not correlated to rugosity (Anton *et al.* 2014; Berjarano *et al.* 2015), however, different environments may be exploited at different strengths and might affect predatory interactions (Alexander *et al*. 2015). Reef habitats with high structural complexity confer a large diversity of light microhabitats (Brakel, 1976; Sheppard 1981; Dinesen 1983). High complexity habitats also provide shading from light which in turn reduces temperature and UVA/UVB exposure (Kelly & Bothwell 2002; Cocheret de la Morinière *et al.* 2004). Light regimes are a key modulator of activity and life events of teleost fish (Downing & Litvak 2001; Cocheret de la Morinière *et al.* 2004). Understanding how predatory behaviour changes with light regimes can indicate vulnerable prey species and give evidence towards potential conservation strategies (Koski *et al*. 2003; Fitzpatrick *et al*. 2013; Ranåker *et al*. 2014). Furthermore, it will allow an insight into understanding the impact of invasive predators at night and on mesopelagic reefs (Bassett & Montgomery 2011). Temperature, structural complexity, and light regimes are intricately linked in coral reef ecosystem dynamics. Reef ecosystems are consequently stressed by perturbations in these factors due to climatic change and alien invasions.

This study therefore aims to apply functional response analysis to determine the magnitude and form of the functional response of lionfish (*Pterois volitans*) and whether it changes with respect to: (1) temperature regime, (2) habitat complexity, and (3) light regimes. We discuss the results with respect to the predictive capacity of functional response analysis to deliver insights into how density dependent resource consumption by lionfish changes under different abiotic scenarios.

2.2 Methods

Trials were conducted in the Queen's University Belfast Marine Laboratory in Portaferry (QML) in January-March 2014 and January-March 2015. Lionfish (6-10cm) were purchased in two batches (n=7, n=6), from Grosvenor Tropicals, Belfast. Specimens were kept in a large tropical marine aquarium holding tank (227l) at 24 ^{o}C and maintained feeding daily *ad libitum* on frozen anchovy. Individuals were acclimated to the tanks for two weeks before starting trials, which typically lasted for two months. Experimental tanks were 34l (45x30x30) tanks which were constantly aerated using a pump and air stone and maintained at 24 ^{o}C. Sand was used as substrate to mimic natural conditions. Fish were left to acclimate in the experimental trials for one hour before prey were introduced. *Paleomonetes varians* (Leach, 1814) (also known as *Palaemon varians*) (Grass shrimp) were chosen as trial prey and supplied from Seahorse aquariums breeding facility. This species was selected to represent a generic prey species and since juvenile lionfish predate largely on invertebrates rather than fish (Cure *et al*. 2012) and due to the successful use of *Paleomonetes spp.* in Cerino *et al.* (2013). Temperature treatments lasted for 24 hours. Habitat and light treatments lasted for 4 hours. Unfortunately, factorial trials were not feasible at this time due to limited predator and prey supply stock.

Temperature trials were run at 22°C and 26°C to simulate the range of temperatures in which lionfish are commonly found (Kimball *et al.* 2004; Schofield 2009; Barker *et al.* 2017). Predators and prey were acclimated to these temperatures for 24hrs before trial. Densities of prey presented were 1, 3, 6, 10 (n=3 per treatment). Habitat complexity trials were carried out with brown plastic pipes (15 x 10cm), which were chosen to mimic lionfish habitat of rocky ledges (e.g., lionfish could rest hanging upside down inside of the pipes), but to also provide shelter for the prey. The arenas either presented as low complexity (no pipes) or high complexity (2 pipes). Densities of prey presented were 1, 2, 3, 5, 7, 10 (n=3 per treatment). Light trials were performed with three different light experimental treatments simulated using light emitting diodes (LEDs). The first light treatment simulated daylight in the tank using white LED lights (WL; using 42 bulbs in total), producing 4.5W with a wavelength ranging from 550-560nm, (Blanco-Vives *et al.* 2012, Fitzpatrick *et al.* 2013). The second light condition was to simulate crepuscular periods using blue LED lights (BL) (38 blue LED light bulbs in total along with 4

white LED lights) to produce the same 4.5W with a wavelength ranging from 450-465nm (Vera *et al.* 2010). Red light (RL) was used to simulate complete darkness (Trippel & Neil 2003), by using a 40W red spot light reflector bulb with a wavelength ranging from 620-630nm. Densities of prey presented were 1, 2, 4, 6, 8, 10, 15, 20, 25 (n=4 per treatment).

Controls were carried out in experimental tanks containing shrimp at each prey density in each treatment, but in the absence of predatory lionfish (n=3 per treatment). Each fish was re-used multiple times, but experienced the density of prey only once to avoid pseudo-replication and the prey density and individual fish were chosen randomly. Fish were given at least 5 days between use and were starved for 3 days prior to experimental procedures to standardize hunger levels.

The R package 'frair' (Pritchard 2014) was used to model the functional response type. Functional responses were modeled using maximum likelihood estimation (MLE; Bolker 2010) and Rogers' (1972) Random Predator Equation (Equation 1.1), due to the prey not being replaced as they were consumed (See 1.3 for analysis details).

The data were non-parametrically bootstrapped (n = 2000) to construct 95% confidence intervals around the mean functional response curve for each treatment. Differences in attack and handling parameters were assessed within treatments using the difference method outlined in Juliano (2001) using the "frair_compare" function in Pritchard *et al.* (2017), with Bonferroni corrections when comparing between three values. All analysis was carried out in R v.3.2.2 (R Development Core Team 2016).

2.3 Results

Prey survival in control groups was >99% in all replicates, therefore any deaths in experimental groups were attributed to predation by lionfish. After addition of the prey, the lionfish would often strike and successfully capture prey within the first minutes of the treatment. Lionfish appeared to be attracted to moving prey rather than stationary prey.

Table 2.1: First order terms and associated *p* values, Functional Response Type, attack (*a*) and handling (*h*) parameter values and *p* values and maximum feeding estimates for all treatments

Treatment	First order term, *p*	Functional Response Type	Attack rate (*a*), *p*	Handling time (*h*), *p*	Maximum feeding estimate (hr^{-1}) (1/*h*T)
22°C	-0.180, 0.06	II	5.29, 0.47	0.28, <0.001	3.6
26°C	-0.223, <0.05	II	4.50, 0.07	0.12, <0.01	8.3
Low complexity	-0.308, <0.001	II	14.36, 0.50	0.34, <0.01	2.9
High complexity	-0.159, <0.05	II	1.27, 0.11	0.26, <0.01	3.8
White light	-0.153, <0.001	II	6.62, <0.001	0.14, <0.001	7.1
Blue light	-0.147, <0.001	II	41.00, <0.001	0.18, <0.001	5.6
Red light	-0.147, <0.001	II	1.99, <0.05	0.23, <0.001	4.3

2.3.1 Temperature Effects

There were significantly more prey consumed at 26°C than at 22°C (t=2.03, df=26.8, p=0.05). Logistic regression had a significantly negative first order term for 22°C and for 26°C, indicating Type II functional responses at both temperatures (Table 2.1, Fig. 2.1). The Type II functional response was significantly higher at 26°C than at 22°C (Table 2.1, Fig. 2.1). There was no significant difference in attack (z=0.10, p-0.91) and handling parameters (z=1.81, p=0.07) between 22°C and 26°C.

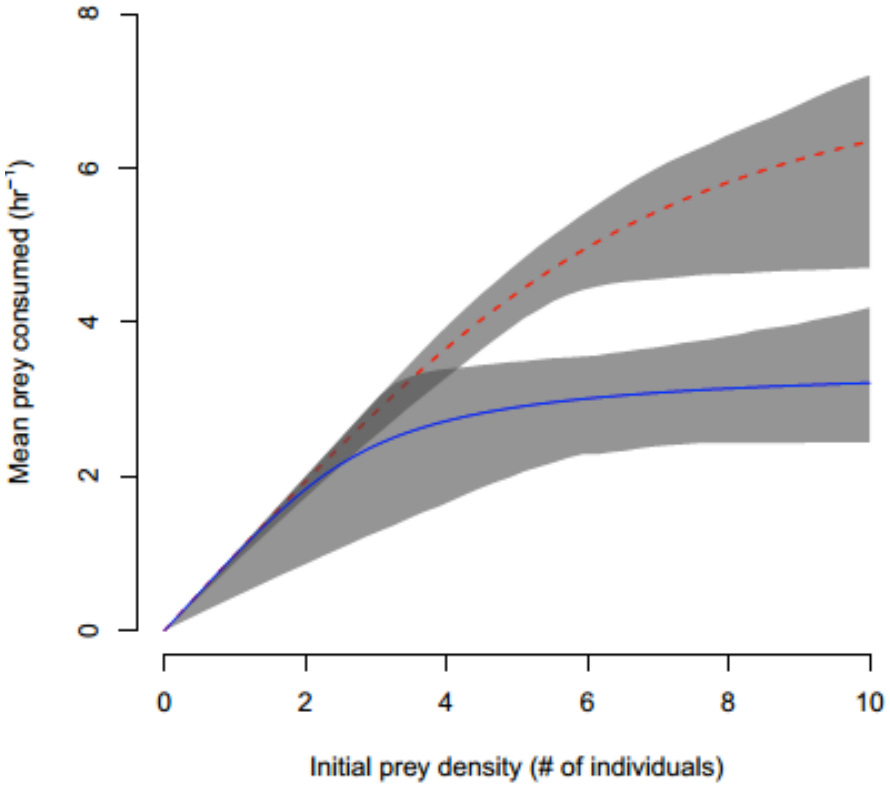


Fig. 2.1 Functional response curves for lionfish at 22°C (blue solid line) and 26°C (red dashed line). Shaded areas are bootstrapped 95% confidence intervals, darker shaded areas indicate overlap

2.3.2 Habitat Effects

There was no significant difference in the number of prey consumed at high habitat complexity compared to low habitat complexity (t=0.94, df=29.9, p=0.35). Logistic regression had a significantly negative first order term for high and low habitat, indicating Type II functional responses for high and low habitat complexity, and the Type II functional responses did not differ significantly between habitat complexity treatments (Table 2.1, Fig. 2.2). There was no significant difference between attack (z=0.59, p=0.55) and handling (z=0.61, p=0.53) parameters between high and low habitat complexity treatments.

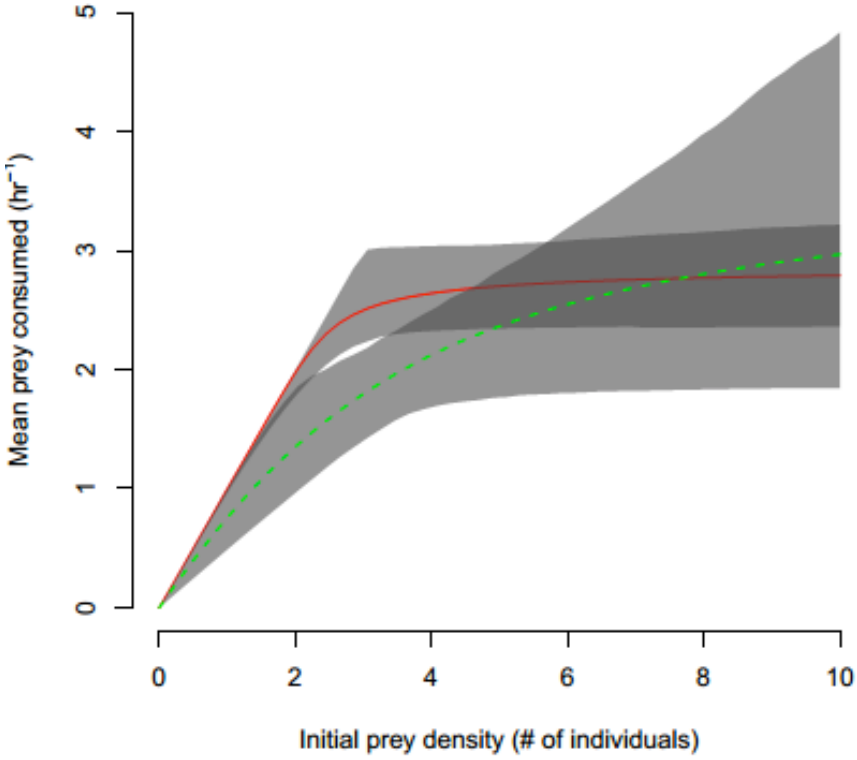


Fig. 2.2 Functional response curves for lionfish at low habitat complexity (red solid line) and high habitat complexity (green dashed line). Shaded areas are bootstrapped 95% confidence intervals, darker shaded areas indicate overlap

2.3.3 Light Effects

There were significantly more prey consumed under blue light than under red light (GLM: $F_{2, 131}$=8.07, z=3.16, p<0.01). There were significantly more prey consumed under white light than under red light (GLM: $F_{2, 131}$=8.07, z=3.83, p<0.001). There was no significant difference in prey consumed between white and blue lights (GLM: $F_{2, 131}$=8.07, z=0.42, p=0.90). Logistic regression first order terms were significantly negative for all light treatments, indicating Type II functional responses (Table 2.1, Fig. 2.3). Type II functional responses under white and blue lights were not significantly different but the functional response under red light was significantly lower (Fig. 2.3). Blue light had the highest attack rate and red light the lowest attack rate (Table 2.1). Attack rates were significantly higher at white light than blue light (z=118469.34, p<0.001) and red light (z=2.46, p<0.05). There was no significant difference in attack rates between blue light and red light (z=1.26, p=0.61). There were no significant differences in handling times between white and blue lights (z=2.03, p=0.12), white and red lights (z=1.96, p=0.14), or between blue and red lights (z=1.34, p=0.53).

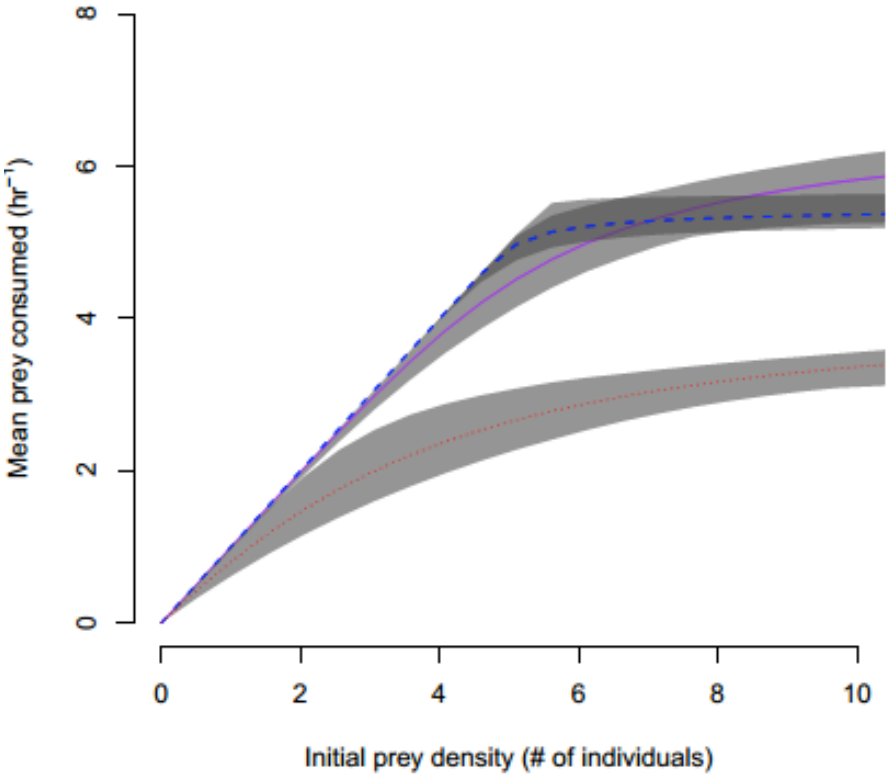


Fig. 2.3 Functional response curves for lionfish for white light (purple solid line), blue light (blue dashed line) and red light (red dotted line). Shaded areas are bootstrapped 95% confidence intervals, darker shaded areas indicate overlap

2.4 Discussion

The ecological impacts of biological invasions can be understood with regards to invader abundance, range and *per capita* effects (Parker *et al*. 1999; Hellmann *et al.* 2008), however, there has been lack of attention to *per capita* effects in general (Dick *et al*. 2014) and under different environmental contexts in particular (Alexander *et al*. 2012; Ricciardi *et al*. 2013; Alexander *et al*. 2015; Iacarella *et al.* 2015; Laverty *et al*. 2015). This has been identified as a gap in invasion ecology knowledge that, if filled, could address prediction of invasive species impacts where there is little invasion history and/or multiple context dependencies (Alexander *et al.* 2014; Laverty *et al.* 2015; Alexander *et al.* 2015). Through understanding how different *per capita* parameters can affect predatory capacity, the information can be incorporated into risk assessments for the entire invaded range (Dick *et al*. 2013), as context effects may create areas of relief or exacerbate interactions (Paterson *et al*. 2014). Many recent studies have shown that the functional response, i.e. *per capita* effect, of invaders is associated with ecological impact. For example, the invasive and ecologically damaging largemouth bass has higher functional responses than native trophic analogues (Alexander *et al*. 2015) and this interaction strength is context dependent (Alexander *et al*. 2015). Juvenile lionfish consistently exhibited Type II functional responses across all three contexts in this study. This high proportional depletion of resources at low resource density is typical of highly damaging invasive predators (Dick *et al.* 2013; Dick *et al.* 2014; Alexander *et al.* 2014; Alexander *et al.* 2015). Furthermore, our results provide a maximum feeding rate for juvenile lionfish under these abiotic contexts, giving a more realistic picture of predator-prey ecological interactions and their strengths.

An increase in temperature, while having little effect on attack rates, lowers the handling time of juvenile lionfish, which increases the maximum feeding rate. This is corroborated by meta-analysis investigating temperature dependencies and scaling on the functional response, whereupon a hump shaped relationship is typical (Englund *et al.* 2011; Rall *et al.* 2012). It is interesting to note that the attack rate between high and low temperature were similar, which suggests that handling rate is the cause for increased impact under high temperatures. Therefore, indicating that a variation in temperature may be driving change in physiological processes more than behaviour (Gilbert *et al*. 2014). Elucidation of these novel *per capita* effects are

important to determine, as context dependent impact assessments are lacking (Iacarella *et al.* 2015), and especially considering forecasting suggests that warming above the thermal optima for a species will decrease interaction strength at *per capita* and population level (Rall *et al.* 2012). Studies have determined lionfish chronic lethal minimum temperature of 10°C and that mean winter temperatures of 14°C and above are predictors of lionfish distribution and density (Kimball *et al.* 2004). However, further temperature trials would be needed to highlight lionfish thermal optima (Iacarella *et al.* 2015), with relevance to functional response magnitude at predicted warming temperatures in the invaded range. Cerino *et al.* (2013) found that the thermal optima for lionfish feeding was 29.8°C, and assessed previous estimations of consumption (Côté & Maljković 2010) to be extremely high (>78% maximum consumption). This is corroborated within our findings, wherein there is high exploitation of prey, especially at low prey densities.

Habitat complexity appears to mediate the impact of damaging alien species in a myriad of ways, as exhibited in previous studies (Barrios-O'Neill *et al.* 2014; Alexander *et al.* 2015). In our study, while both complexities revealed a Type II response; low complexity had a non-significantly higher attack rate, while high complexity had a non-significantly lower handling time. This can be attributed to habitats with a high degree of structural integrity limiting a predator's efficiency by interfering with detection of prey and the ability of the predator to catch the prey (Greene 1986; James & Heck 1994; Alexander *et al.* 2015; Barrios-O'Neill *et al.* 2015). This occurs through a variety of mechanisms; the formation of a physical barrier causes disruptive implications for visual (Manatunge *et al.* 2000; Warfe & Barmuta 2004) and olfactory signals (Ferner *et al.* 2009), furthermore physical structure can provide complete or partial refuge for prey from predators (Finke & Denno 2006; Horinouchi 2007). In addition, a predator's ability to manoeuvre within a structure is often impaired (Winfield 1986; Bartholomew *et al.* 2000; Barrios-O'Neill *et al.* 2015). Therein, it is a general assumption that the foraging efficiency of predators ought to decrease with increasing habitat complexity (Radomski & Goeman 2001; Alexander *et al.* 2015), thus effectively dampening the strength of the functional response. This said, habitat complexity could work to facilitate predation (Marinelli & Coull 1987). This can occur through within refuge competition between prey (Orrock *et al.* 2013) and utilization of structure by predator; such as lionfish using overhanging structures for ambush predation (Biggs & Olden 2011). This may

explain the shorter handling time and therefore, higher maximum feeding rate, in the higher complexity habitat despite having a lower attack rate. Habitat is thus thought of as an important mediator in predator-prey interactions (Alexander *et al.* 2012). Investigating the effect of habitat complexity using fractal dimensions and predator free space (Barrios-O'Neill *et al*. 2015) may provide further insight into the effects of structure in lionfish predation.

Light regimes are a strong modulator of animal behaviour (Schwalbe & Webb 2015). Reef fish often have strong circadian rhythms, which manifest as periods of crepuscular feeding (Helfman 1986; Domeier & Colin 1997). In the white light (daylight proxy) the fish exhibited the highest attack and lowest handling times, which translated in the highest consumption rates. The blue light proxy for crepuscular periods exhibited a steeper initial functional response incline than the other light treatments. The handling time was lowest under blue light, which supports the notion of persistent crepuscular feeding due to a decrease in predator avoidance although, none of the handling times in the light treatments differed significantly. These results differ from the predation rates calculated by Côté and Maljković (2010), which determined that lionfish predation is more successful under overcast conditions. However, this study did not assess predation under crepuscular light conditions. There are contrasting reports on the feeding behaviour of lionfish, some suggesting all day feeding (Morris & Akins 2009; Côté & Maljković 2010), while other evidence reports that crepuscular feeding is conserved in the invaded range (Jud & Layman 2011; Cure *et al.* 2012). Our results indicate that feeding will occur throughout a range of light wavelengths, albeit at significantly lower levels during dark periods. The behaviour relates to a trade- off between predator visual acuity and predator avoidance by prey in low light levels (Cure *et al.* 2012). Individual movement and hunting behaviour was less under red light (*personal observation*). This has been noted in other species (Koski & Johnson 2002), as a reduction in swimming reduces energy costs thus allowing more to be put into growth and reproductive effort (Appelbaum & Kamler 2000); this works in the benefit of lionfish as it is a slow swimming, ambush predator (Albins & Lyons 2012). The comparative functional response was significantly lower in red light than under the white and blue light regimes; this suggests that the impact of the invasive lionfish will be lower in deep, dark water (Nuttall *et al.* 2014), especially when combined with the finding that the impact of the invasive lionfish is reduced in dark periods and in colder water.

Further studies should pinpoint the light wavelengths at mesophotic reefs to understand the relevant impact at depth, as phase shifts to algal dominated communities have been documented on a Bahamian mesophotic coral reef in response to the lionfish invasion (Lesser & Slattery 2011; Andradi-Brown *et al*. 2017), which suggests that despite the reduced impact in comparison to under other light regimes, there is still disproportionally higher resource consumption compared to native predators.

Functional response analysis has been used in this instance as a proxy for invader impact on native resources (Alexander *et al.* 2012; Alexander *et al.* 2014; Dick *et al.* 2014). The form of the functional response, in this case Type II, can be used to predict the measure of change the lionfish population may be exerting on prey populations (Ward *et al.* 2008; Jeschke *et al.* 2014) and therefore coral and temperate reef ecosystems. Invasive species exhibiting a Type II functional response have the capacity to drive prey populations to local extinctions if prey are unable to match predator consumption rate with recruitment (Sinclair *et al.* 1998; Twardochleb *et al.* 2012; Alexander *et al.* 2014). In this case it seems that lionfish consistently and successfully feed at a high percentage of their daily ration (Cerino *et al.* 2013), which thus poses a considerable threat to biodiversity and commercial fisheries. When managing damaging invaders, after pinpointing what species are most at risk, it is essential to identify the interplay between biotic and abiotic factors and how the environment mediates predator-prey interaction strengths. While the present study is not factorial, it highlights factors that have the capacity to mediate predation impact. The main mechanism identified here revolves around the ability of lionfish to locate prey rather than handling limitations. However, temperature remains a pervasive driver for invasion success by mediating handling rates and thus maximum feeding rates through physiological mechanisms. Unfortunately, this is a factor that cannot be mitigated by local management. Nonetheless, due to the high exploitation of low prey densities by lionfish, management should focus on the conservation of rare species by moderation of other pressures such as fishing and habitat destruction. Currently, prevention of marine invasions is becoming increasingly futile due to connectivity and other human mediated changes in the abiotic environment, therefore it is important to develop the predictive capacity of novel uses of functional response analysis in cohesion with other trait based methodologies so as to combat the

invasive impact of alien species (Parker *et al*. 1999; MacNeil *et al.* 2013; Dick *et al*. 2014).

Chapter 3

The functional response of the intertidal Shanny, *Lipophrys pholis*: effects of prey supply and temperature

Data was collected as part of a MSc. project supervised by J. South. All data analysis and write up was completed by J. South.

Data from this chapter has been accepted for publication:

South, J., Welsh, D., Anton, A., Sigwart, J., Dick, J.T.A. Increasing temperature decreases the predatory impact of the intertidal shanny (*Lipophrys pholis*) on an amphipod prey. *Journal of Fish Biology*

3.1 Introduction

Climate change is recognised as the most pervasive driver of global variation on several scales (Halpern *et al*. 2008; Doney *et al*. 2009; Doney *et al*. 2012; Duarte 2014). Increasing temperatures are an observable consequence of anthropogenic climate forcing, with a predicted average temperature rise of 3°C or more (SNIFFER UKCC13 2007). The strengths of predator-prey interactions and environmental productivity are more than likely to change and alter ecosystem stability (Hiscock *et al*. 2004; Casini *et al*. 200; Gilbert *et al*. 2014).

Temperature will also have an effect at the individual level (Vasseur *et al*. 2014), whereupon the metabolism of organisms is increased and leads to changes in behaviour (Rummer *et al*. 2013; Dell *et al*. 2014). It is hard to predict how species will respond to climate change due to the number of life stages and differences within them, nonetheless, changes are already occurring as a product of anthropogenic forcing (Le Quesne & Pinnegar 2012). Changes in environment may cause native species to develop traits through abiotic mediation of physiology and behaviour that are destructive, as *per capita* consumption is expected to increase with temperature (Englund *et al*. 2011; Dell *et al*. 2014). However, the success of a species within the new ecological parameters depends upon the tradeoff between the species physiological limits and the adaptational and ecological constraints (Peck *et al*. 2009).

It is important to build experimental datasets to quantify and predict predator impact under different contexts and using a range of different organisms (Gilbert *et al*. 2014; Dell *et al*. 2014). Using functional response as a prediction tool in climate change ecology provides a quantifiable metric that can be used across a variety of contexts (Andersen *et al.* 2004; Dick *et al.* 2013). It is feasible that the same prediction methodology will be transferable to understanding native species responses to environmental perturbations.

Predation is considered a key factor affecting community structure and ecosystem function (Sih *et al*. 1985; Woodward *et al*. 2010; Stevnbak *et al*. 2012; Cahill *et al*. 2013). Using ubiquitous species as proxies and model species on which to investigate the effects of climate change on predator prey interaction strengths will allow insight into possible mechanisms and outcomes of the inevitable climatic future. The shanny, (*Lipophrys pholis*; Linneaus, 1758), is a common intertidal

blenniid that is integral to the trophic dynamics of rocky shore systems (Mazé *et al*. 1999; Dodd *et al*. 2000; Lima *et al*. 2008). Individuals colonise tidal pools, but can also be found across wide areas of the shore (Faria & Almada 2006), where they withstand tidal cycles by retreating into holes and crevices. Due to the ubiquity of *L. pholis* on rocky shores and its potential effects on community structure in the intertidal trophic web, it is an ideal model experimental species; this is further supported by its resilience, small size and ability to be kept successfully in aquaria (Davenport & Woolmington 1981; Milton 1983). *Lipophrys pholis* could also be considered as a proxy or exemplar for other native rocky shore fish species. The prey of such species include amphipods, which are universally associated with the littoral zone (Karez *et al*. 2000; Duffy & Harvilicz 2001). Littoral amphipods such as *Echinogammarus marinus* (Leach, 1815) are typically mesograzers (Dick *et al*. 2005) and can have large impacts upon community structuring across a range of trophic levels (Duffy & Hay 2000; Maranhão *et al*. 2001; Haggitt & Babcock 2003; Dick *et al*. 2005; Kelly & Dick 2005). Furthermore, *E. marinus* is an effective indicator species due to its prevalence, susceptibility to abiotic perturbation and its importance as a prey species to higher trophic levels (Múrias *et al*. 1996; Leite *et al*. 2014). *E. marinus* is an important prey species of *L. pholis* and other marine intertidal species, thus is a sympatric species and therefore will experience the same perturbations to environment as *L. pholis.* In addition, *Echinogammarus. marinus* is easily caught, kept in aquaria and quantified, and therefore is fitting to use as an experimental prey species.

This chapter will assess whether the functional response of *L. pholis* changes with temperature increase. The temperatures investigated are representative of current summer temperatures and the forecasted temperatures for Strangford Lough in 2050 and 2080. Furthermore, an assessment of functional response methodologies will be completed to see whether there are discrepancies in the results produced when prey is not replaced (Dick *et al*. 2013) and when prey is replaced after consumption (Alexander *et al*. 2012). This will inform against potential biases within the models for which future studies can consider.

3.2 Methods

Climate change assumptions were generated from data from Table 3.2 UKCIP02 Climate Change Scenarios for Northern Ireland (SNIFFER UKCC13 2007), which states that sea surface temperature (SST) will increase by +1°C in the 2020s, +0.5±1.5°C in the 2050s and +1.0±2.5°C in the 2080s. Current SST temperatures were found from the Agri-Food Biosciences Institute database (AFBI, 2016). Within Strangford Lough, current winter temperature averaged at 7°C and the summer temperature averaged at 15.5°C in 2014. Therefore, the temperatures chosen reflect the current summer temperature of 15°C, temperatures in 2050s of 17°C, and temperatures in 2080 of 19°C (SNIFFER UKCC13 2007; Sokolov *et al.* 2009).

Lipophrys pholis and *Echinogammarus marinus* specimens were collected from the inter-tidal zone from Walter Shore, Portaferry, Co. Down, Northern Ireland (54°23'27.3" N 5°33'54.4" W). *Lipophrys pholis* specimens were transferred to a holding tank (432 L, 120 x 60 x 60 cm) with a flow through system at Queen's University Belfast Marine Laboratory (QML) and were maintained on crushed mussels and fed *ad libitum* every other day. *Echinogammarus marinus* were transferred to two 45 L tanks with constant flow through seawater, and maintained on *Laminaria digitata* replaced once a week. Specimens were kept in holding tanks for 2 months prior to experimentation so as to acclimate them to lab conditions and feeding regimes.

Experiments were completed in outdoor aquariums in January 2015. Five prey densities were investigated at three different temperatures. Controls were *E. marinus* in experimental arenas at each prey density at each temperature in the absence of predators (n=3). Temperature was measured using digital thermometers. Water was heated using 50 W thermostatic aquarium heaters to create water baths in 45 L boxes with two 10 L arenas per box. Each arena was fitted with an airline bubbling continuously. Each bucket held one fish, fish were introduced into the buckets for two days to acclimate to their surroundings, and during this period the fish were each fed one mussel. After two days the seawater was exchanged and the heaters were turned on to their assigned temperatures. The fish were left to acclimate for a further two days to acclimate to the experimental temperature before the experimental replicates were run and during this time, the fish were starved to achieve a standardised hunger level. Each box was covered with a dark lid

to simulate usual feeding conditions and to exclude rain water. Experimental trials ran for six hours, from 09.00-16.00, these times were chosen as they spanned a range of tidal times. Replicates were run across three days to allow for randomization of temperature regime, suitable recovery and acclimation between re-use. This randomization allowed all three temperatures and the five prey densities to be run simultaneously. Fish were measured to the nearest 0.5 cm total length (9.2±1.3SD cm). Fish were re-used 3 times, but were never exposed to the same procedures (i.e. prey density and temperature) more than once. Prey densities used were 2, 5, 10, 15, 20 (n=4 per temperature treatment). Prey size range was 5-10 mm. Prey were allowed to acclimate to experimental temperatures over the course of 24h before the replicates were run. All fish were returned alive to the collection site after use.

3.2.1 Prey supply models and analysis

There were two models of prey supply. Fish were supplied with their assigned density of prey at the beginning of each replicate but the prey were not replaced following consumption. Each replicate was disturbed by removing and replacing a small amount of water in the arena to mimic the level of disturbance of the prey replacement model. Replicates were checked every hour and any prey eaten were replaced to the original starting density.

All analyses were carried out in R v.3.3.0 (R Development Core Team 2016). FR Type was determined using models accounting for prey depletion (Equations 1.1, 1.2, 1.3) and prey replacement (Equation 1.4 and 1.5). Data were non-parametrically bootstrapped (n=30) to generate multiple estimates of attack rate, handling time and maximum feeding rate. Generalized linear models (GLM), with quasi-poisson error distribution to account for over dispersion, were used to test for differences in quantity of prey consumed and bootstrapped parameters within prey supply models at each temperature for replacement and non-replacement models. Tukey honest significant difference post-hoc tests were used to generate multiple comparisons. T-tests were then completed to determine differences between the quantities of prey consumed and bootstrapped parameters across model type and temperature.

Suitability of each model was compared with Akaike Information Criterion (ΔAIC). Functional responses were then fitted using maximum likelihood estimation (MLE; Bolker 2010) and the Lambert W function (Bolker 2008). Data were also

non-parametrically bootstrapped to generate bootstrapped clouds (n=2000) (Barrios-O'Neill *et al*. 2014, 2015).

3.3 Results

Control prey survival was >99% and thus prey mortality in the experimental groups was due to predation. Fish behaviour was similar to that observed in sitú whereupon movement was limited unless disturbed. During acclimation periods a large amount of milky mucus substance was produced from many individuals, which was then discarded with water changes every day.

3.3.1 Prey consumed

There was a significant difference in the number of prey consumed among the three temperatures in the non-replacement model (GLM: $F_{2, 57}$=3.58, p<0.05; Fig. 3.1a). There were significantly more prey consumed at 15°C than at 19°C (z=2.54, p<0.05) (Fig. 3.1a). There was no significant difference in the number of prey consumed among the three temperatures in the replacement model (Fig. 3.1a). There was no significant difference between the number of prey consumed at 15°C between non-replacement and replacement models. There were significantly more prey consumed in the replacement model than in the non-replacement model at 17°C (t=2.75, p<0.01), and at 19°C (t=3.75, p<0.01) (Table 3.1, Fig. 3.1a)

3.3.2 Attack Rate

There were significant differences between the attack rates in the non-replacement model (GLM: $F_{2, 62}$=4.08, p<0.05) (Table 3.1, Fig. 3.1b). The attack rates were significantly higher at 15°C than at 19°C (z=2.55, p<0.05), and at 17°C than 19°C (z=2.31, p=0.05; Table 3.1, Fig. 3.1b). There was no significant difference between 15°C and 17°C (Table 3.1, Fig. 3.1b). There was a significant difference between the attack rates at each temperature in the replacement model (GLM: $F_{2, 76}$=80.36, p<0.001). The attack rates were significantly higher at 15°C than at 17°C (z=6.64, p<0.001), 15°C than at 19°C (z=12.49, p<0.001), and at 17°C than at 19°C (z=6.69, p<0.001). There were significantly higher attack rates in the non-replacement model compared to the replacement model at 15°C and at 17°C (Table

3.1, Fig. 3.1b). There was no significant difference in attack rates at 19°C between non-replacement and replacement.

3.3.3 Handling time

There was a significant difference between the handling time between temperatures in the non-replacement model (GLM: $F_{2, 62}$=25.82, p<0.001; Table 3.1, Fig. 3.1c). The handling time was significantly shorter at 15°C than at 19°C (z=5.73, p<0.001; Table 3.1, Fig. 3.1c), and at 17°C than 19°C (z=5.25, p<0.001; Table 3.1, Fig. 3.1c). There was no significant difference between handling times at 15°C and 17°C (Table 3.1, Fig. 3.1c). There was no significant difference between 15°C and 17°C. There was a significant difference between the handling time at each temperature in the replacement model (GLM: $F_{2,76}$=40.69, p<0.001; Table 3.1, Fig. 3.1c). The handling times were significantly shorter at 15°C than at 17°C (z=6.15, p<0.001; Table 3.1, Fig. 3.1c), and significantly longer at 17°C than at 19°C (z=8.09, p<0.001; Table 3.1, Fig. 3.1c). There was no significant difference between handling time at 15°C than at 19°C. Non-replacement models had significantly longer handling times at 15°C and at 19°C (Table 3.1, Fig. 3.1c). There was no significant difference in handling time at 17°C between model types.

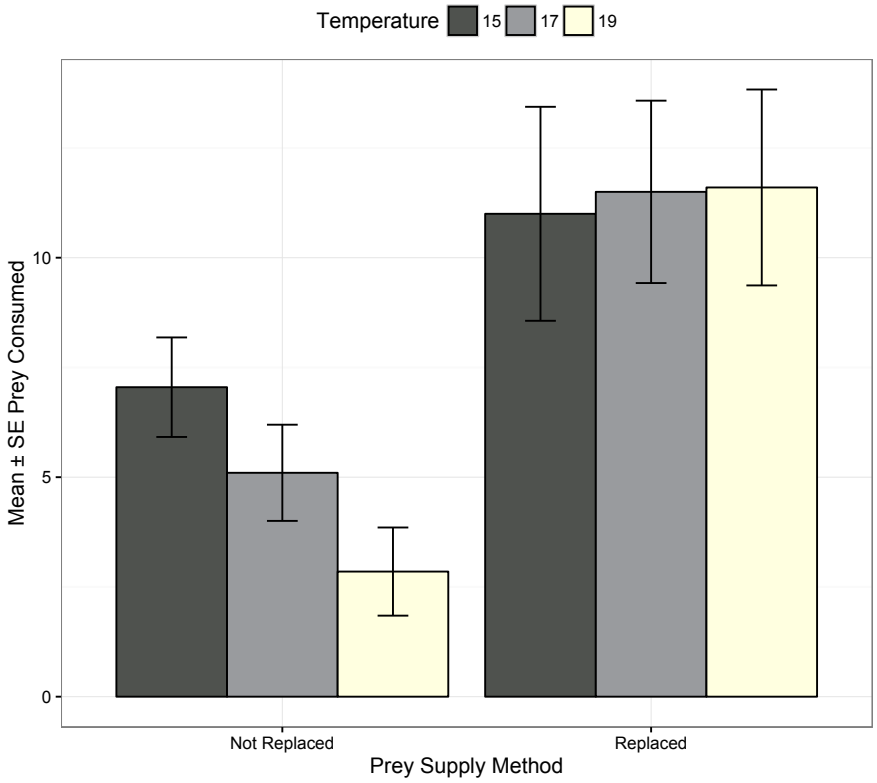
3.3.4 Maximum feeding estimate

There was a significant difference between maximum feeding rate in the non-replacement model (GLM: $F_{2, 62}$=6.51, p<0.01; Table 3.1, Fig. 3.1d). There were significantly higher maximum feeding estimates at 15°C than at 19°C (z=2.79, p<0.05; Table 3.1, Fig. 3.1d). There were significantly higher maximum feeding estimates at 17°C than at 19°C (z=3.23, p=0.01; Table 3.1, Fig. 3.1d). There was no significant difference between maximum feeding estimates at 15°C and 17°C (Table 3.1, Fig. 3.1d). There was a significant difference between the maximum feeding estimates at each temperature in the replacement model (GLM: $F_{2, 76}$=103.68, p<0.001; Table 3.1, Fig. 3.1d). The maximum feeding estimate was significantly higher at 15°C than at 17°C (z=7.06, p<0.001) and at 19°C (z=11.60, p<0.001; Table 3.1, Fig. 3.1d). The maximum feeding estimate was significantly lower at 17°C than at 19°C (z=7.28, p<0.001; Table 3.1, Fig. 3.1d). Maximum feeding estimates were higher in the replacement model at 15°C and 19°C (Table 3.1, Fig. 3.1d). At 17°C

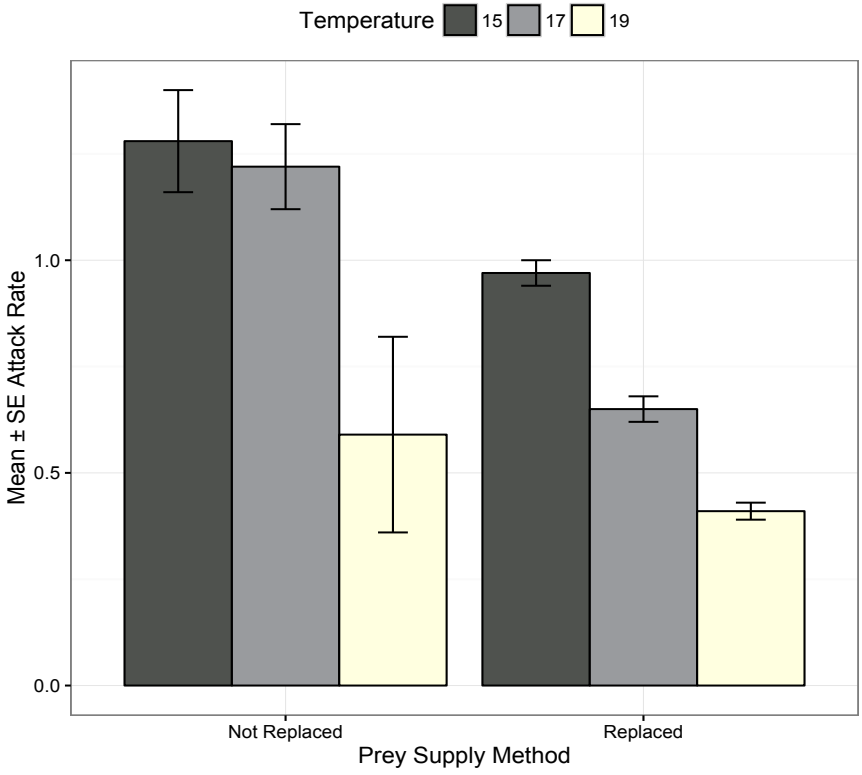
the non-replacement model had significantly higher maximum feeding estimates (Table 3.1, Fig. 3.1d).

Table 3.1 Mean±SE of prey consumed, attack rate (*a*), handling time (*h*), and maximum feeding estimate (1/*h*T) for each temperature treatment in the non-replacement and replacement methods

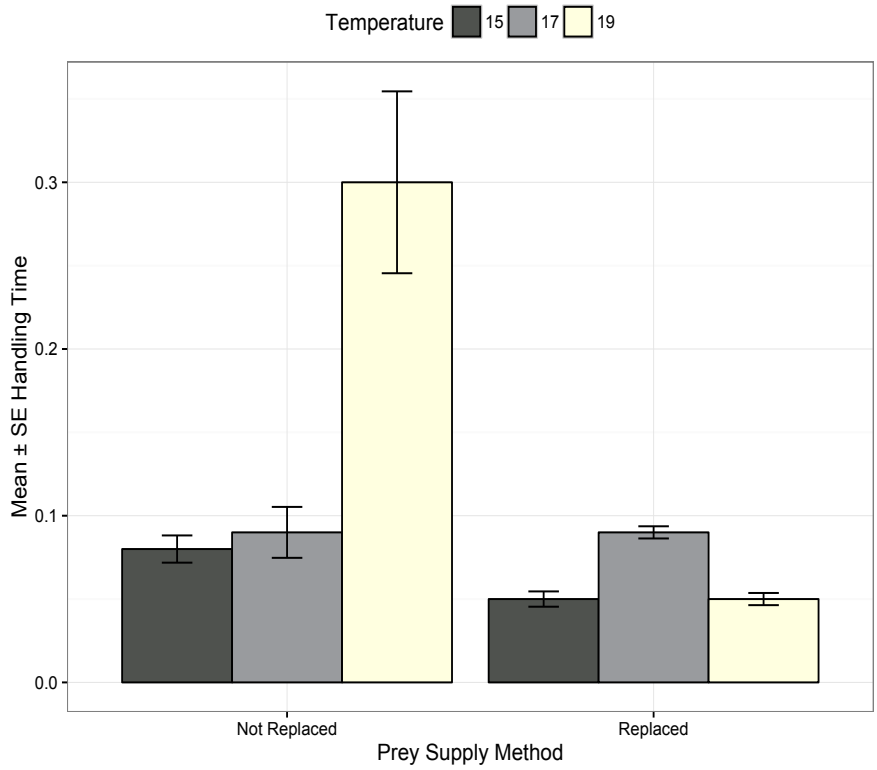
Prey Consumed				
	Non-Replacement	Replacement		
Temperature (°C)	Mean±SE	Mean±SE	t	*p*
15	7.05±1.13	11.00±2.43	1.46	0.15
17	5.10±1.09	11.50±2.07	2.75	<0.01
19	2.85±1.00	11.6±2.23	3.57	<0.01
Attack rate (*a*)				
	Non-Replacement	Replacement		
Temperature (°C)	Mean±SE	Mean±SE	t	*p*
15	1.28±0.12	0.97±0.02	2.60	<0.05
17	1.22±0.09	0.64±0.02	5.68	<0.001
19	0.62±0.24	0.40±0.02	0.97	0.34
Handling time (*h*)				
	Non-Replacement	Replacement		
Temperature (°C)	Mean±SE	Mean±SE	t	*p*
15	0.08±0.01	0.05±0.00	3.17	<0.01
17	0.09±0.01	0.09±0.02	0.25	0.79
19	0.32±0.05	0.04±0.02	5.02	<0.001
Maximum feeding estimate (1/*h*T)				
	Non-Replacement	Replacement		
Temperature (°C)	Mean±SE	Mean±SE	t	*p*
15	17.2±2.20	26.44±3.59	2.60	<0.05
17	19.6±3.14	11.82±0.62	2.43	<0.05
19	7.6±3.08	2.72±0.16	7.80	<0.001


Temperature
15
17
19
Mean ± SE Prey Consumed
10
5
0
Not Replaced
Replaced
Prey Supply Method

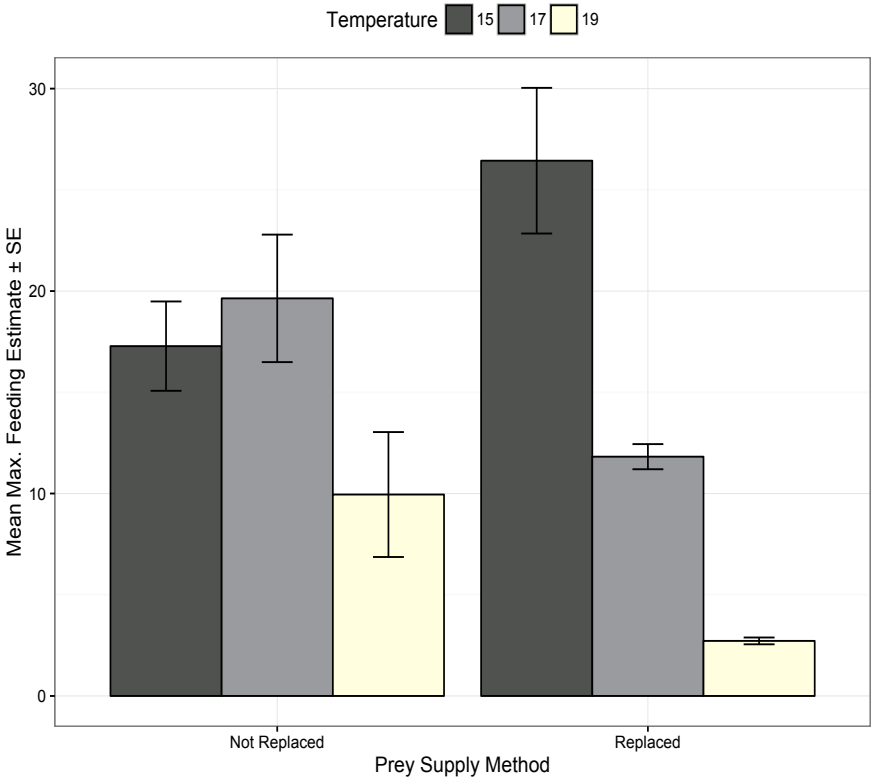
3.1a


Temperature
15
17
19
Mean ± SE Attack Rate
1.0
0.5
0.0
Not Replaced
Replaced
Prey Supply Method

3.1b



3.1c



3.1d

Fig. 3.1 Mean ± SE of bootstrapped parameter values at each temperature and prey replacement method for **a**) Prey consumed, **b)** Attack Rate, **c)** Handling Time, **d)** Maximum Feeding Estimate (hr^{-1})

3.3.5 Functional Response

The non-replacement model and the replacement model at 15°C had a Type II functional response as signified by the significantly negative first order terms from the logistic regression. Bootstrapping indicates a high degree of overlapping, which suggests that the functional response from each prey supply model is not significantly different (Table 3.2, Fig. 3.2a).

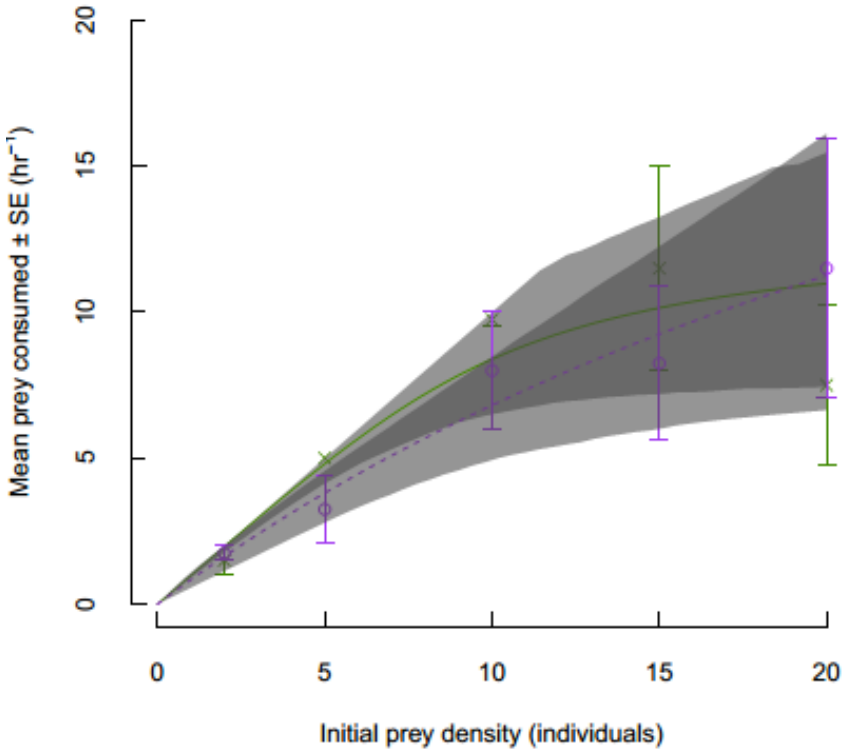
The non-replacement model at 17°C produced non-significant terms from the logistic regression and GLM. This could be interpreted as a Type I response but due to the stipulations described in Jeschke *et al.* (2004) it was modeled as a Type II functional response. The replacement model at 17°C had a significantly negative first order term from the logistic regression but the GLM had non-significant negative first and second orders which indicated an intermediate Type II/III functional response which was modeled using a flexible model. There was a high degree of overlap in the bootstrapped data, which indicates that the responses modeled were not significantly different between prey supply models (Table 3.2, Fig. 3.2b).

The non-replacement model at 19°C had a non-significant first order from the logistic regression but significantly negative first order and significantly positive second order terms was the GLM which indicate a Type III functional response. The replacement model at 19°C had a non-significant positive first order term from the logistic regression. The first order term from the GLM was non-significantly positive and the second order term was non-significantly negative, this suggests an intermediate Type II/III functional response and therefore was modeled using a flexible model. There was a small degree of bootstrap overlapping at low and high densities but the models diverged considerably at the middle densities (Table 3.2, Fig. 3.2c).

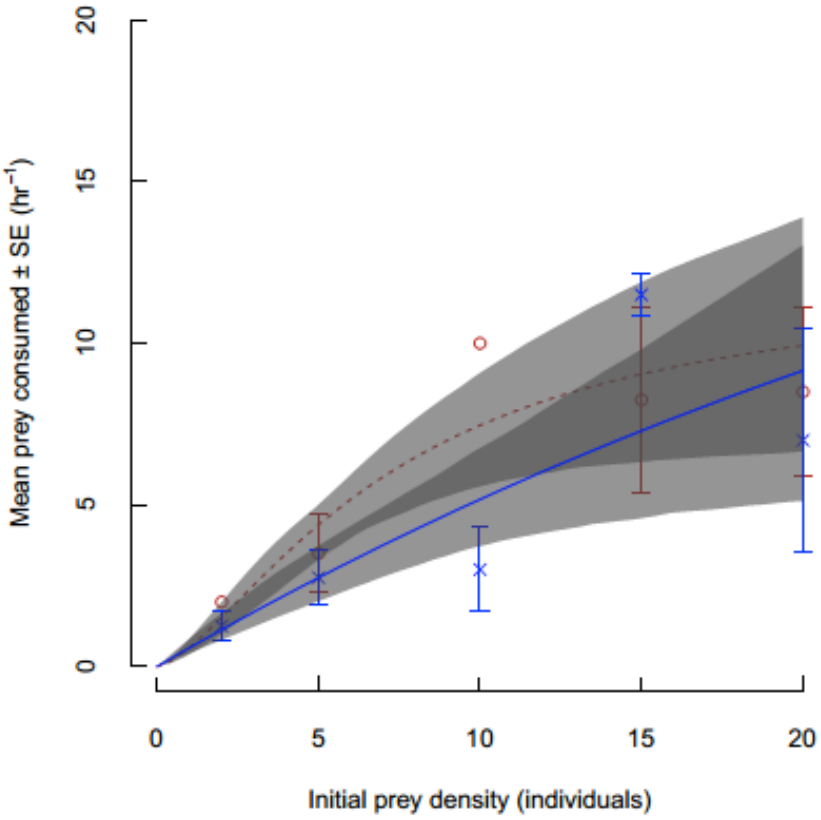
Table 3.2 Functional response types determined from logistic regression, and first and second order terms reported for all temperatures and replacement and non-replacement trials

Treatment	Log. Reg. First order term, (*p*)	GLM First order term, (*p*)	GLM Second order term, (*p*)	Functional Response Type
15nr	-0.290, (<0.001)	0.289, (0.13)	-0.020, (<0.001)	II
17nr	-0.028, (0.26)	0.194, (0.12)	-0.008, (0.07)	II
19nr	0.027, (0.34)	-0.510, (<0.001)	0.021, (<0.001)	III
15r	-0.061, (<0.05)	-0.103, (0.47)	0.001, (0.76)	II
17r	-0.175, (<0.001)	-0.032, (0.84)	-0.005, (0.40)	II/III
19r	0.004, (0.86)	0.127, (0.33)	-0.004, (0.347)	II/III

3.2a


Mean prey consumed ± SE (hr^{-1})
0
5
10
15
20
Initial prey density (individuals)

3.2b


Mean prey consumed ± SE (hr^{-1})
0
5
10
15
20
0
5
10
15
20
Initial prey density (individuals)

3.2c

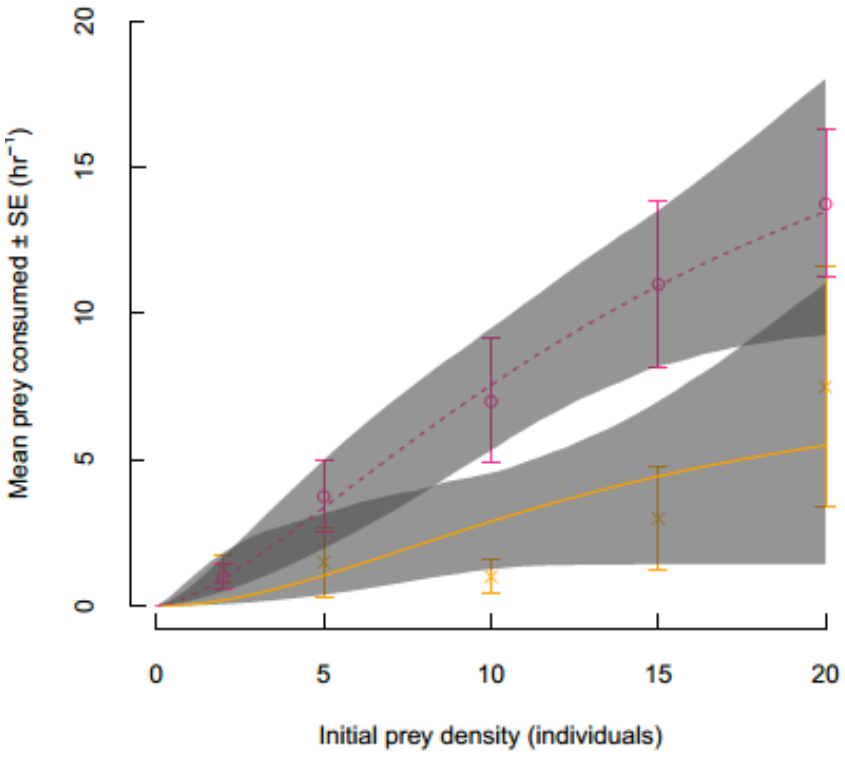


Fig 3.2 Functional response curves with 95% confidence intervals. Shaded areas indicate bootstrapping (n2000) to 95% confidence intervals. Dark areas indicate overlapping. **3.2a**: 15°C replacement (dashed line) and non-replacement (solid line). **3.2b**: 17°C replacement (dashed line) and non-replacement (solid line). **3.2c**: 19°C replacement (dashed line) and non-replacement (solid line)

3.4 Discussion

Predicting the potential change in trophic interaction strengths is both important and confounding (Peck *et al*. 2009; Grigaltchik *et al*. 2012). An increase in temperature should theoretically increase foraging demands in poikilotherm fish due to an amplified metabolic rate (Gilbert *et al*. 2014). However, the results obtained from this experiment suggest a more complex reality. Data from the present study showed the functional response of a model predator-prey system under short-term temperature increase and highlighted how temperature change can elicit a change in predatory behaviour.

When considering consumer – resource dynamics, both predator and prey response must be considered. An increase in temperature should theoretically increase foraging demands in a poikilotherm due to an amplified metabolic rate (Gilbert *et al*. 2014). In the prey non-replacement model, there were more prey consumed at 15°C than at 19°C. While both species are resilient inter-tidal species (Milton 1983), the temperature ranges for *E. marinus* are from 5.4-31.7°C (Leite *et al*. 2014), which is far higher than the 17.5°C optimal temperature for the northerly distributed *L. pholis* (Horn & Gibson 1990, Francisco *et al*. 2011). Having to adapt to adverse conditions can reduce predatory impact (Kitching 1977) and thus may dampen predatory impact in this system. This is supported by Davenport and Vahl (1979) wherein 16°C was highlighted as the peak temperature for consumption of seaweed in *L. pholis.* There was no difference in the number of prey consumed between temperatures in the replacement model, presumably due to the nature of the treatment, wherein prey were repeatedly supplied but the predator did not reach satiation. The present study and the results of Alexander *et al*. (2012) show similar trends wherein the replacement models had significantly more prey consumed, although this was only revealed at 19°C. The number of prey consumed should not be considered solitarily as a reliable estimator of impact.

Some sources attest that attack rate should not vary with temperature and therefore, variation in resource consumption is attributed to the thermal dependence of the handling time (Dell *et al*. 2011), others report hump shaped parameter relations with temperature change (Englund *et al*. 2011), and increases in attack rate with temperature increase (Rall *et al*. 2012). The parameters suggest that in this case, attack rate is affected by temperature. It is unclear through what mechanism, as there

was a concomitant decrease in attack rate with the increase in temperature. This directly contrasts with other studies wherein activity, consumption and strike rate were increased by increasing temperature (Biro *et al*. 2010; Nowicki *et al*. 2012; Allan *et al*. 2015); however, the attack rates in these previous studies were not investigated under varying prey densities. Differing responses could be due to differences in tropical and temperate fishes under thermal stress (Rummer *et al*. 2013) and differences in organism lifestyle and foraging regime, as the study organism *L. pholis* is an intertidal omnivore (Milton 1983). There was a significantly higher attack rate in the replacement model carried out by Alexander *et al*. (2012), which was not seen within this study. In the instance of the replacement model, the encounter rate of prey is increased and therefore gives an underestimation of attack rates compared to the non-replacement model (Kerr 1974; Plat & Denman 1978, Sih & Moore 1990).

Both organisms used in this study are resilient inter-tidal species (Milton 1983), the temperature ranges for *E. marinus* are far higher than the 17.5°C recorded optimal temperature for the northerly distributed *L. pholis* (Horn & Gibson 1990; Francisco *et al*. 2011, Leite *et al.* 2014). In the present experiments, air was bubbled through the system to avoid oxygen limitation, but we did not measure dissolved oxygen within the experimental arenas. There is a concomitant decrease in aerobic ability with an increase in temperature due to the twin issues of decreasing capacity of warmer water to hold dissolved oxygen and insufficiency of the animals' circulatory and ventilator systems (Pörtner & Knust 2007). Previous work has shown differences in attack rate and capture success when predator and prey have different optimal performance temperatures (Dell *et al*. 2014; Gilbert *et al*. 2014, Pawar *et al*. 2015). Furthermore, there is a decrease in activation energy for 'negative movement' such as prey escape (Dell *et al*. 2011). At higher temperatures, prey use less energy to escape than they would at lower temperatures (Dell *et al*. 2011). Having to adapt to adverse climatic conditions can reduce predatory impact (Kitching 1977). Thus, *L. pholis* may be more negatively affected by the temperature change than the prey species, which gives it a disadvantage at higher temperatures.

The handling parameter in the models used takes into account the time spent pursuing prey, time spent processing prey, and time spent in digestive pause (Holling 1968, Hassell 1978). The non-replacement model showed a trend of increased handling time with increased temperature. This seems to go against the

understanding that increased temperature is predicted to decrease handling time due to increased metabolic rate of the predator (Jeschke *et al.* 2002; Dell, Pawar & Savage 2011). As such it could be inferred that a thermal stress response was triggered by the comparably rapid warming scenario, which involved some degree of fasting due to the decrease in oxygen at higher temperatures affecting metabolism processes (Brown *et al*. 2004, Pörtner & Knust 2007). However, as noted previously, the experimental design allowed for adequate acclimation to temperature (2 days) and all experimental temperatures are well within the normal range experienced by these species in regular short term thermal excursions in littoral environments. The experimental design only accounts for consumption of prey and not potential changes in escape behaviours.

The comparative study by Alexander *et al*. (2012) showed no difference between handling rates between the prey supply models. The present study showed there was a significant trend of higher handling rates within the non-replacement models at 15°C and 19°C which could be explained by the potential model overestimation of handling times as the handling parameter could arguably be further broken down into more specific processes as handling and physiological digestion have different thermal parameters (Sentis *et al*. 2013) but are combined in this model. Digestive pause only occurs when the predator is fed to satiation (Mills 1982), which does not occur during the non-replacement models as there were significantly more prey consumed in the replacement models across all temperatures. Thus, the handling time is often over estimated due to the combination of active and physiological processes within one parameter (Dell *et al.* 2011; Sentis *et al*. 2013). The overall predator-prey interaction in the experimental data can be considered an accurate reflection of responses under the experimental temperatures, it is not possible to make any conclusion about whether decreased predation in higher temperatures is specifically due to lower capture success of the predator, or increased prey escape success.

The maximum feeding rate estimates for non-replacement and replacement models showed similar trends of decreasing with increasing temperature as this is derived from the handling parameters. The non-replacement model diverges from the replacement model at 17°C wherein the maximum feeding rate is slightly higher than 15°C. This suggests that the predator is at peak performance between these two temperatures (Davenport & Vahl 1979). The replacement model decreases in

maximum feeding rate as the temperature increases, but due to not reaching satiation point over the course of the experiment the maximum feeding rates may be higher. Furthermore, a longer acclimation time may affect the maximum feeding rate as the predator adjusts to the new conditions (Kitching 1977).

Both non-replacement and replacement models elicited a shift in functional response type, from Type II to Type III with an increase in temperature. However, a difference was seen in the magnitude intensity of the functional response curve of each temperature between the prey supply models. In the non-replacement model, there was a negative trend with functional response intensity decreasing with increasing temperature, this contrasts with other studies done on invertebrate systems (Wasserman *et al.* 2016). These results are counter-intuitive to what was expected due to *Lipophrys pholis* being poikilothermic and thus, temperature having a direct effect on physiological processes.

Boldness in an individual is increased by temperature and motivational state (Stephens & Krebs 1986; Cuthill & Houston 1997; van Baalen *et al*. 2001; Nowicki *et al*. 2012). When hungry, fish exhibit enhanced boldness due to an augmented motivational state; this causes them to become more vulnerable to predators and less selective towards prey until threshold fullness is satisfied (Ariyomo & Watt 2015). This may be seen in the non-replacement results wherein an increased motivational state explains the Type II response at 15°C and 17°C but the transition into a Type III sigmoidal response at 19°C may be a thermal threshold, which could incite fasting behaviour as a reaction to thermal stress (Brown *et al*. 2004) until there are higher densities of prey supplied which would make foraging more beneficial under the optimal foraging theory (Stephens & Charnov 1982; Lang *et al.* 2017). However, the replacement model produced results indicating a positive trend of the increase of functional response intensity with increasing temperature. The number of prey consumed between the replacement models were not significantly different from each other. It should be considered that if there was higher initial prey densities supplied, differences between prey consumed and maximum-feeding estimates may be revealed along with a change in functional response type. Furthermore, replacement style experiments ought to be related back to the environmental context of predator and prey abundance (Plat & Denman 1978; Sih & Moore 1990), wherein amphipods are highly abundant but under exploited in preference of sessile species (Milton 1983; Mazé *et al*. 1999; Faria & Almada 2006; Silva *et al*. 2010). The

differences between the functional response shapes in the replacement model, compared to non-replacement, could be attributed to the fish being more likely to reach satiation at lower densities due to the patch being replenished. Therefore, the predator experienced a greater range of motivational and physiological states (Clark & Mangel 2000).

Within experiments of this type there is usually hope to speculate upon potential adaptive pathways as a response to climatic drivers. However, reductive controlled laboratory experiments are evidentially not reflective of long-term climatic change (Welch e*t al*. 2014). As such they cannot realistically highlight evolutionary mechanisms or broad scale community interactions. It is not intentional to undermine these experimental results, but only to emphasize the context in which data can illuminate biological processes. Acute warming is a poignant issue (Peck *et al*. 2009), especially in systems that already represent extreme physiological stress. In littoral marine environments, which are model systems for ecology, tidepools and isolated shallow waters are prone to intense warming periods in summer months. The merit in this study is that a short-term picture of the physiological responses and interactions of model species and their reactions to rapid thermal stress is revealed. This highlights individual variation and limitations in respect to foraging capacity (Spicer & Gaston 1999; Peck *et al*. 2009; Calosi *et al*. 2013). Metabolic responses and individual variation is essential to consider when attempting to gather a more complete understanding of the complex interactions involved in climate forcing (Brown *et al*. 2004; Melatunan *et al*. 2013). As such, individual based, laboratory experiments are a first step, and a powerful tool to comprehend and quantify interactions. The variations in results between prey supply models highlight the need to continue to improve prediction models.

As a comparative study, the emphasis is on the difference between parameters rather than the absolute value (Alexander *et al*. 2012). This paper highlights the effect of short-term acclimation and temperature change on a common intertidal teleost predator. Results suggest that predatory impact will ultimately be dampened by short-term high temperature increases, potentially due to a dampening of the attack rate. Nonetheless, due to the high maximum feeding rate and low handling time observed at 17°C there may be periods of intense and destabilising predation in the near future before mean local sea surface temperatures exceed this predator species' optimum at 17.5°C (Davenport & Vahl 1979; Horn & Gibson

1990; Francisco *et al*. 2011). This has implications for intertidal food webs and productivity as predation may decrease during periods of sharp temperature rise. With consistent temperature rise, the effects may be more ecologically damaging. Further work is essential to correctly understand how changing abiotic parameters will affect consumer-resource dynamics in the future if there is to be an attempt to predict and manage resource flux.

Chapter 4

A diet comparison of a commercial (Gadhus morhua) and non-commercial predator (Scyliorhinus canicula) with regards to substrate type in the Irish Sea

4.1 Introduction

Description of fish diet via gut content analysis has been done in a multitude of studies (Reñones *et al*. 2002; Joyce *et al*. 2002; Domi *et al*. 2005; Pepin 2006; Baker *et al*. 2014; Romeo *et al*. 2015). In doing so the researcher is able to put together a snapshot of diet composition and therefore infer nuances of consumer-resource interactions (Armstrong 1982; Hop *et al*. 1992; Bax 1998; Olaso 1998; Bascompte *et al*. 2005; Smout & Lindstrøm 2007). This is a necessary part of fisheries management and takes into account a whole ecosystem approach to sustainability, wherein different species are considered as part of a dynamic system that impact upon one another (Daan, 1973; Murawski 2000; Borja *et al*. 2014). The Irish Sea (ICES VIIa) is a system that is utilised for commercial activities (Richardson 2016) and contains populations of many commercial and non-commercial species (Kelly *et al*. 2006; Heath *et al*. 2012; Pinnegar *et al*. 2015). It is a complex system as species can be both predator and prey within the same functional group, therein overfishing or a change in predator prey interaction intensity could lead to a "cultivation/depensation" quirk (Walters & Kitchell 2001). This is where an increase of small pelagic species leads to increased predation on cod (and other large predatory species) eggs and larvae thus halting recovery. Dynamics such as this are common in pelagic landscapes as juveniles of top predators may be preyed upon by adults of species that would be prey in the future. As such, predation is a key driver in structuring oceanic and coastal food webs (Sih *et al*. 1985; Pace *et al*. 1999). It is prudent to be aware of the intensity of predator prey interactions between both commercial and non-commercial species (Ney 1990) and to assess which prey species are most integral to diet and whether there is a possibility of economically and biologically adverse cascade effects leading from conservation of a particular species (Daan 1973). This is in concurrence with the notion that the ideal sampling should sample both predator and prey concurrently to understand the effect of resource availability (Jolicoeur & Brunel 1966).

Marine environments are subject to a variety of stochastic forces which cause variation in community dynamics controls (Jennings & Kaiser 1998; Fromentin *et al*. 2001). Two drivers of which are climate forcing and fishing pressure (Cochrane *et al*. 2009; Brander 2010). Thus, community composition is constantly in some degree of flux (Bellard *et al*. 2012) and this poses a difficulty for fisheries management as

policy needs to constantly be under review to ensure maximum sustainability and economic output. Baseline studies are useful to illustrate the state of a system, with regards to community composition, health and interactions but baselines are now considered as moving, due to the degree of change in recent decades (Certain & Planque 2015; Mcclanahan & Graham 2015). While population studies are carried out in the Irish Sea area bi-annually, there are few recent studies that describe the diet composition and quantify the predator-prey interactions of trophically important predators in the Irish Sea. This is necessary for efficient fisheries management to understand how different populations affect each other, and to assess the resource utilisation and partitioning between predators (Ellis *et al*. 1996; Quevedo *et al*. 2009).

Habitat selection in commercial fisheries is a factor for fisheries exploitation (Fréon & Misund 1999). The Irish Sea comprises of a variety of substrate types (see Appendix 1), which provide integral habitats to species of economic importance (Howard & Bennett 1979; Rogers 1992; Amezcua & Nash 2001). Habitat complexity and type are important factors in interaction strength as they can provide refuge for both predator and prey (Scharf *et al.* 2000; Tupper & Boutilier 2011), and facilitate resource abundance as productive habitats are selected for by predators (Sims 2003; Berlow *et al*. 2008). Therefore, understanding the degree of habitat utilisation for resource consumption is necessary to inform management on areas of importance.

Many methods have been employed in the past to thoroughly assess and quantify predator diet and predator – prey interactions. These often include using a cohort of metrics to give a balanced picture of prey selection (see Strauss 1979 and Liao *et al*. 2001), however, Baker *et al.* (2014) purport that frequency of occurrence is the most robust measure of diet composition as volumetric methods tend to give incorrect credence to unusual, large, and hard to digest prey items (Hyslop 1980; Walters 1997; Baker *et al.* 2014). However, it would be an oversight to use only one metric, such as frequency of occurrence, as the size and weight of prey items is informative of prey selection. Therefore, a bulk analysis is an efficient way to characterise predator diet without introducing too much inherent bias.

Cod (*Gadhus morhua*) are a valuable commercial, mixed fisheries species (Richardson 2016) and are on the IUCN red list as a vulnerable species (Sobel 1996). Cod are a pan-Atlantic species and favour water with an annual mean of 12°C (Dutil & Brander 2003; Drinkwater 2004). They are a benthopelagic species and can be

caught between depths of 50-400m (Drinkwater 2004). There have historically been huge fluctuations in cod populations as a result of overfishing (Myers *et al.* 1996; Katz *et al*. 2009). Removal of large predators could cause an imminent trophic cascade as macroinvertebrates increase with the crash of cod populations (Frank *et al*. 2005). The Northern Irish (NI) cod fishery has decreased in value by 77% while the tonnage caught also decreased by 49% however, the value per tonne increased by 69% in the Jan-March period of 2015 compared to the same period of 2014 (Richardson 2016). Despite the reduction in tonnage caught the catch constitutes mainly immature individuals less than 3 years (O'Brien *et al*. 2000; Richardson 2016). This compounds upon the already reduced yearly cohorts and reproductive capacity that has been in an unsustainable situation in the Irish Sea since 2002 (Richardson 2016).

Dogfish are a small, benthic, catshark species which can be found abundantly across the North-East Atlantic and the Mediterranean Sea. They inhabit a range of depths; from the sub-littoral to continental shelves (Ellis *et al*. 2005). Dogfish are not a targeted fishery; however, a substantial amount is landed every year (Richardson 2016). This is because dogfish are taken as bycatch from trawl fisheries (Revill *et al* 2005; Rogriguez-Cabello *et al* 2005). Nonetheless, dogfish exhibit a high discard survival rate (Revill *et al* 2005; Rogriguez-Cabello *et al* 2005). Populations of dogfish are stable and increasing in the Irish Sea (Richardson 2016). Catsharks (*Scyliorhinidae*) are ideal model species for identifying shark behaviours and ecology; they are large enough to be tracked and caught in the field, but are small enough to be maintained within laboratory conditions (Sims 2003). They are particularly tractable for studying diet as they have a slow digestion rate and a propensity for regurgitating food (Sims 1996; Andrews *et al*. 1998).

The intention of this Chapter is to begin to elucidate upon the habitat selection of a commercial (cod) and non-commercial (dogfish) predator; assess whether there is a difference in resource consumption with different habitat substrates with regards to which prey items are the most important to each species; the scale of niche overlap between predators; to assess whether there is predatory pressure on the commercially valuable *Nephrops* fishery; and to identify differences in prey selectivity. Ideally this will shed light upon the ecology of two ecologically important predators in the Irish Sea and contribute to informing the continuously moving baseline. Additionally, it may provide information that could be used to

inform policy and fisheries management to maintain sustainability, biodiversity and local economy.

4.2 Methods

4.2.1 Sampling

Data were collected over 02/03/15-22/03/15 during Agri-Food Biosciences Institute's (AFBI) March groundfish survey on the RV Corystes in the Irish Sea. (See Appendix 1. for specific haul details and locations). Note: Station 345 is on the map as 250, however the actual sample location was moved slightly due to a wind farm being built on the station. Stations were grouped for analysis by substrate type. The gear used was a commercial Rockhopper otter trawl fitted with a 20mm liner in the cod-end. Cod end was 60mm mesh size and increasing from 80mm to 120mm to the wings. Cod (n=118) and dogfish (n=78) individuals above 40cm were picked randomly from the subsamples taken for processing within the groundfish survey. Size range was chosen to account for maturity and gape/stomach size as larger specimens have prey that is more easily identifiable and prey sizes that would be represented within the trawl survey. Cod stomachs were removed and immediately frozen in a blast freezer due to requirements for other biological processing on board, whereas dogfish samples were frozen whole in the blast freezer. All samples were brought back to AFBI laboratories for analysis.

4.2.2 Analysis

Gut contents were grouped into predator species, station location and substrate type. Prey species were identified to species and genus level if possible. Items were then condensed into categories for analysis as commercial fish species, non-commercial fish species, commercial invertebrates and non-commercial invertebrate species.

Commercial fish species: plaice (*Pleuronectes platessa*), herring (*Clupea harrengus*), sprat (*Sprattus sprattus*), whiting (*Merlangius merlangus*), mackerel (*Scomber scombrus*), haddock (*Melanogrammus aeglefinus*), witch (*Glyptocephalus cynoglossus*), thick back sole (*Microchirus variegatus*). Non-commercial fish species: common dragonet (*Callionymus lyra*), Norway pout (*Trisopterus esmarkii*), dab (*Limanda limanda*), long rough dab or American Plaice (*Hippoglossoides*

platessoides), fries goby (*Lesuerigobius friessii*), pipefish (*Syngnathinae sp.*). Dab were included in this category due to being generally ignored as a targeted fishery in favour of other flatfish species. Commercial invertebrate species: queen scallop (*Aequipecten opercularis/Chlamys opercularis*), *Cancer pagurus*, *Crangon crangon, Nephrops norvegicus*. Non-commercial invertebrates: anemone (*Actiniaria sp.*), *Aphrodita aculeata*, brittle star (*Ophiurida sp.*), *Corystes cassivelaunus*, hermit crab (*Pagurus spp.*), *Pandalus borealis*, *Pasiphaea multidentata*, *Sepiola sp.,* swimmer crabs (*Liocarcinus spp.*), turretshell (*Terebridae sp.*), topshell (*Gibbula umbilicalis*), *Polychaeta spp., Xantho pilipes*, squat lobster (*Galathea sp.*).

T tests, Generalised Linear Models (GLMs) and Kruskal-Wallis analysis of variance tests were completed on data using Tukey's Honest Significant Difference post-hoc tests.

Length, sex, gut weight (g) and total number of items in the gut were recorded. Stomach fullness was recorded visually as a metric from 1-6 per methods used in Hop *et al*. (1992). Fullness was further quantified and corrected for to consider variation in individual length using methods developed by Darbyson *et al*. (2003) (Equation 4.1), wherein; I_F is length corrected fullness, c is the stomach content mass and L is fish length.

$$I_F = 10000c\ L^{-3} \qquad \textbf{Equation 4.1}$$

Digestion state was also recorded as a metric from 0-3; empty (0), no digestion prey still identifiable (1), partially digested but prey still identifiable (2), entire digestion prey unidentifiable asides from small hard parts such as otoliths (3).

Percentage Geometric Index of Importance ($\%GII_i$) (Equation 4.5) and percentage Index of Relative Importance ($\%IRI_i$) (Equation 4.6) were calculated for each prey item to determine the difference in prey importance for each predator. These consider the percentage composition of each prey species by number ($\%N_i$) (Equation 4.2), the percentage weight composition of prey species ($\%W_i$) (Equation 4.3) and the percentage frequency of occurrence ($\%FO_i$) of each prey species (Equation 4.4).

$\%N_i =$ $\frac{(No.\ of\ prey_i)}{(Total\ no.\ of\ all\ prey)} * 100$ **Equation 4.2**

$\%W_i =$ $\frac{(Weight\ of\ prey_i)}{(Total\ weight\ of\ all\ prey)} * 100$ **Equation 4.3**

$\%FO_i =$ $\frac{(No.\ stomachs\ with\ prey_i)}{(Total\ stomachs\ with\ prey)} * 100$ **Equation 4.4**

$\%GII_i =$ $(\%N_i + \%W_i + \%FO_i)$ **Equation 4.5**

$\%IRI_i =$ $(\%N_i + \%W_i) * \%FO_i$ **Equation 4.6**

Schoener's Index (Schoener 1968, 1970) of dietary overlap (Equation 4.7) was carried out on the frequency of occurrence of taxa in cod and lesser-spotted dogfish gut contents. Frequency of occurrence was used rather than weight as using weight can give too much credence to larger items.

$D = 1 - 0.5 \sum_{i=1}^{n} |P_{x,i} - P_{y,i}|$ **Equation 4.7**

Where D is Schoener's index of niche overlap, $P_{x,I}$ and $P_{y,I}$ are the proportions of resource category *i* utilised by species x and y, and *n* is the number of resource categories

Environmental data were collected as part of the groundfish survey as the trawl gear was optimised to survey for predator and prey species concurrently. These data detailed frequency of occurrence, weight, frequency and length of all potential prey species that were caught in the trawls at each station. Prey species in the environment >21cm were not included in the analysis due to gape restrictions of dogfish and the length of the predators that were being caught. These data were broken down into percentage abundances of each prey category in the environment for each substrate type. Percentage abundance of each prey category found in cod and dogfish stomachs was also calculated for each substrate type.

The Shannon - Weaver Index of diversity (Shannon 1948) (Equation 4.8), – hereafter referred to only as the Shannon Index (See Spellerberg & Fedor 2003 for issues pertaining to origins) – was calculated for the environmental data and gut

content data to provide comparative community composition overall and on different substrate types. This index describes the entropy of a community.

$$(H) = \sum_{i=1}^{s} p_i \ln p_i \qquad \textbf{Equation 4.8}$$

Where H is the Shannon diversity index, H has no bound upper value, Σ is the total number of species in the community, P_i is the proportion of S made up of the *i*th species. Unidentifiable prey taxa were omitted from this analysis.

Ivlev's (1961) Index (Equation 4.9) was used to quantify the selectivity shown for different prey items and prey categories by cod and dogfish.

$$E = (r_i - p_i)/(r_i + p_i) \qquad \textbf{Equation 4.9}$$

Where *E* is Ivlev's Index, r_i is the relative abundance of a prey item in diet and p_i and n_i are the relative abundance of a prey item in the environment. This information was calculated from the environmental data on prey species collected during the survey. Ivlev's index has values ranging from +1 to -1. +1 indicating that a prey item is eaten more than proportionally, given its relative abundance in the environment, thus being strongly selected for, and -1 indicating strong negative selection. 0 represents random feeding and that a prey item is eaten as it is encountered. Unidentifiable items and items such as algae, plastic and fish fry species were not included in this analysis as sampling for abundance of these in the environment was not possible or ingestion was considered to be incidental.

4.3 Results

In the entire survey, 504 cod and 3510 dogfish were caught, from this, a total of 118 cod stomachs and 78 dogfish stomachs were sampled. The mean length of cod was 53.20cm while the mean length of dogfish sampled was 53.50cm. There were significantly more dogfish caught than cod ($t=2.78$, $df=19$, $p<0.05$; Table 14, Fig. 4.1). There was no significant difference in the lengths of cod and dogfish sampled ($t=0.17$, $df=194$, $p=0.86$; Table 4.1). There was no significant difference in length between male and female cod ($t=0.96$, $df=85.10$, $p=0.33$; Table 4.1) or between male and female dogfish ($t=1.93$, $df=24.84$, $p=0.06$; Table 4.1). Therefore, the samples

were not biased by size difference. There were significantly more dogfish caught on gravel than cod (X^2=6.81, df=1, p<0.01; Table 4.1, Fig. 4.1). Differences in number of cod and dogfish caught mud, sand and silt, and mixed substrates were non-significant (Table 4.1, Fig. 4.1).

The mean weight in the gut was 18.15±3.30g for cod and 30.07±2.67g for dogfish (Fig. 4.2). Dogfish had significantly heavier gut contents than cod (GLM: $F_{1,194}$=9.09, p<0.01; Fig. 4.2). There was no significant interaction between predator and substrate and sex (GLM: $F_{2,181}$=0.42, p=0.65; Fig. 4.2). Female cod had significantly heavier gut contents than males (GLM: $F_{1,116}$=6.80, p<0.05; Fig. 4.3), as did female dogfish (GLM: $F_{1,76}$=5.38, p<0.05; Fig. 4.3).

In total, there were 244 items found in cod gut contents, and 148 items found in dogfish gut contents (Fig. 4.4). The mean number of items found in cod gut contents was 2.06±0.28 and then mean number of items found in dogfish gut contents was 1.89±0.18. There was no significant difference in the number of prey items in cod and dogfish gut contents (GLM: $F_{1,194}$=0.21, p=0.64; Fig. 4.5) or between substrate and cod and dogfish gut contents (GLM: $F_{3,188}$=0.26, p=0.84; Fig. 4.5).

Unidentifiable teleosts made up 24.6% (n=60) of cod stomach contents while this category only represented 6.08% (n=9) in dogfish. *Merlangius merlangus* were the most frequent fish found in both species stomach contents; representing 13.5% (n=33) of prey in cod gut contents and 6.7% (n=10) in dogfish gut contents, followed by *Callionymus lyra*; 3.2% (n=8) in cod gut contents and 3.3% (n=5) in dogfish gut contents (Fig. 4.4). *Pandalus borealis* were the most frequent invertebrate found 21.7% (n=53) in cod gut contents but only constituted 3.3% (n=5) in dogfish gut contents (Fig.4. 4). *Nephrops norvegicus* was the most frequent invertebrate found in dogfish gut contents 14.8% (n=22) and 3.6% (n=9) in cod gut contents (Fig. 4.4). Both species consumed swimmer crabs (*Liocarcinus spp.*), which made up 4.5% (n=11) of prey in cod gut contents and 6.0% (n=9) in dogfish gut contents (Fig. 4.4).

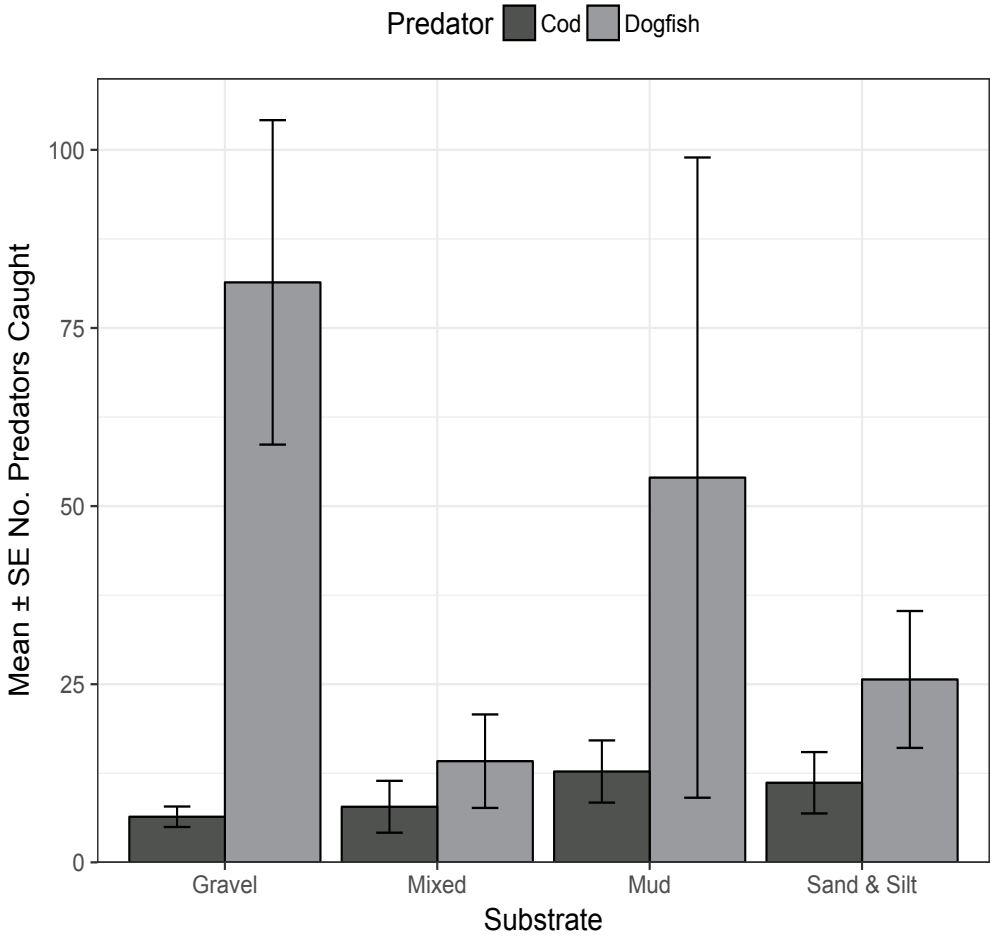


Fig. 4.1 Mean ± SE No. predators caught on each substrate

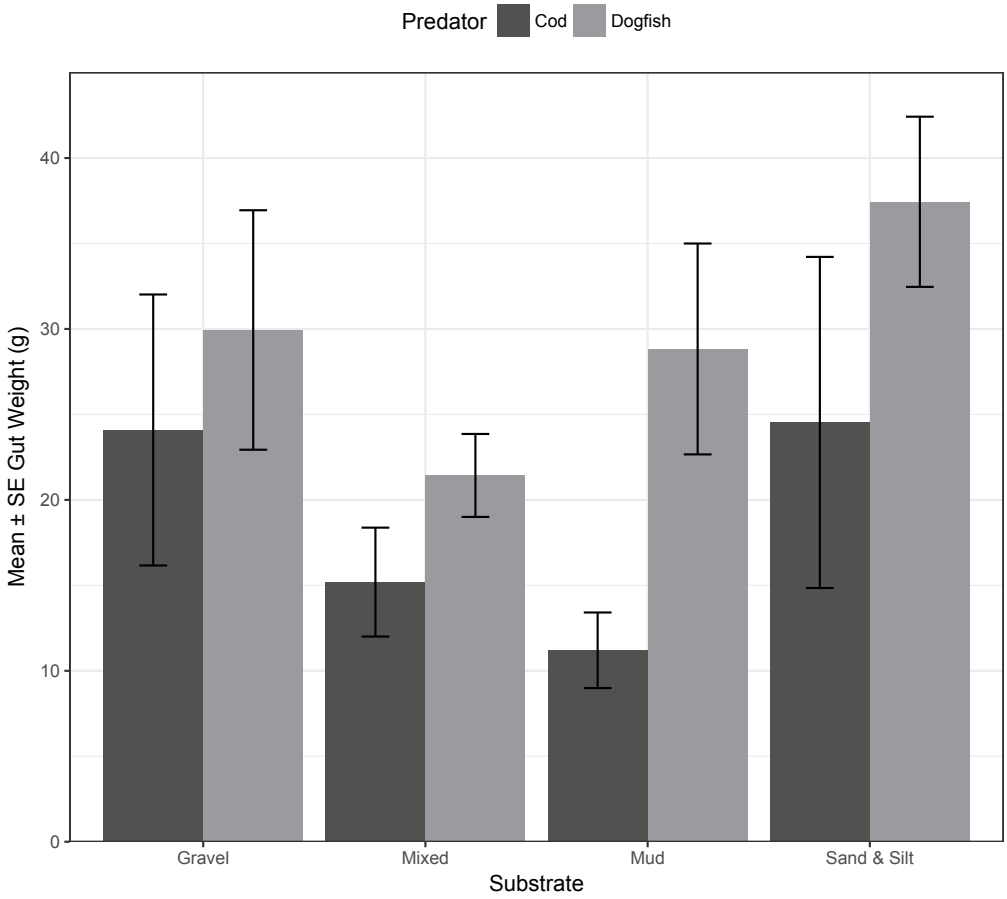


Fig. 4.2 Mean ± SE predator gut weight (g) on each substrate

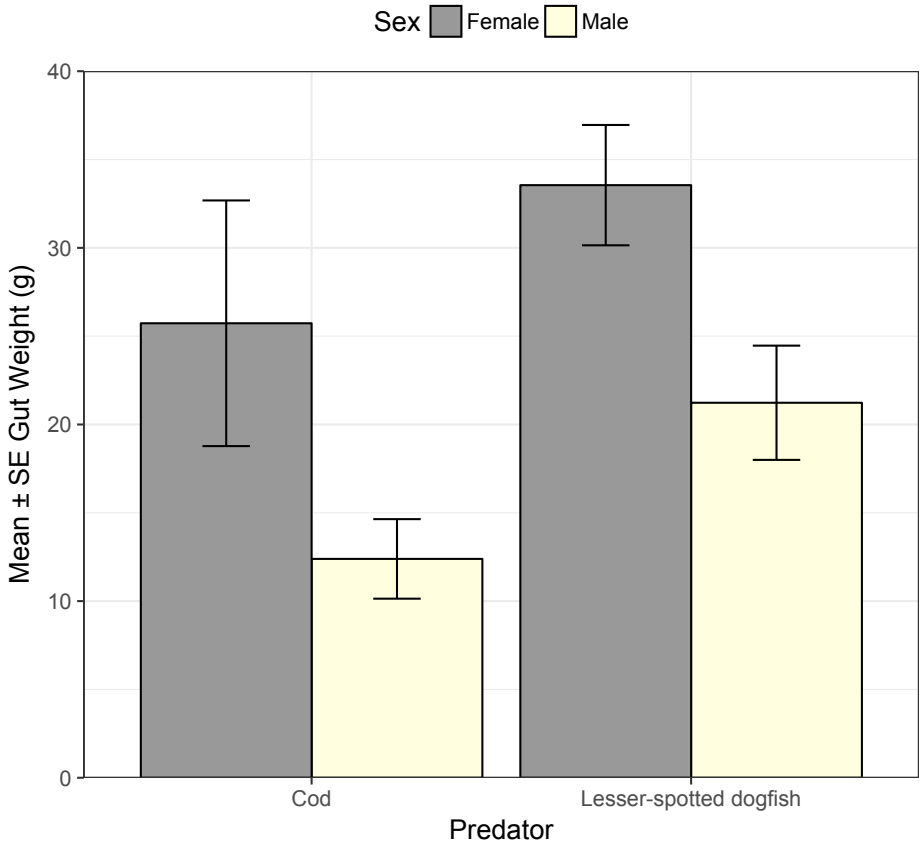


Fig. 4.3 Mean ± SE predator gut weight (g) between sexes

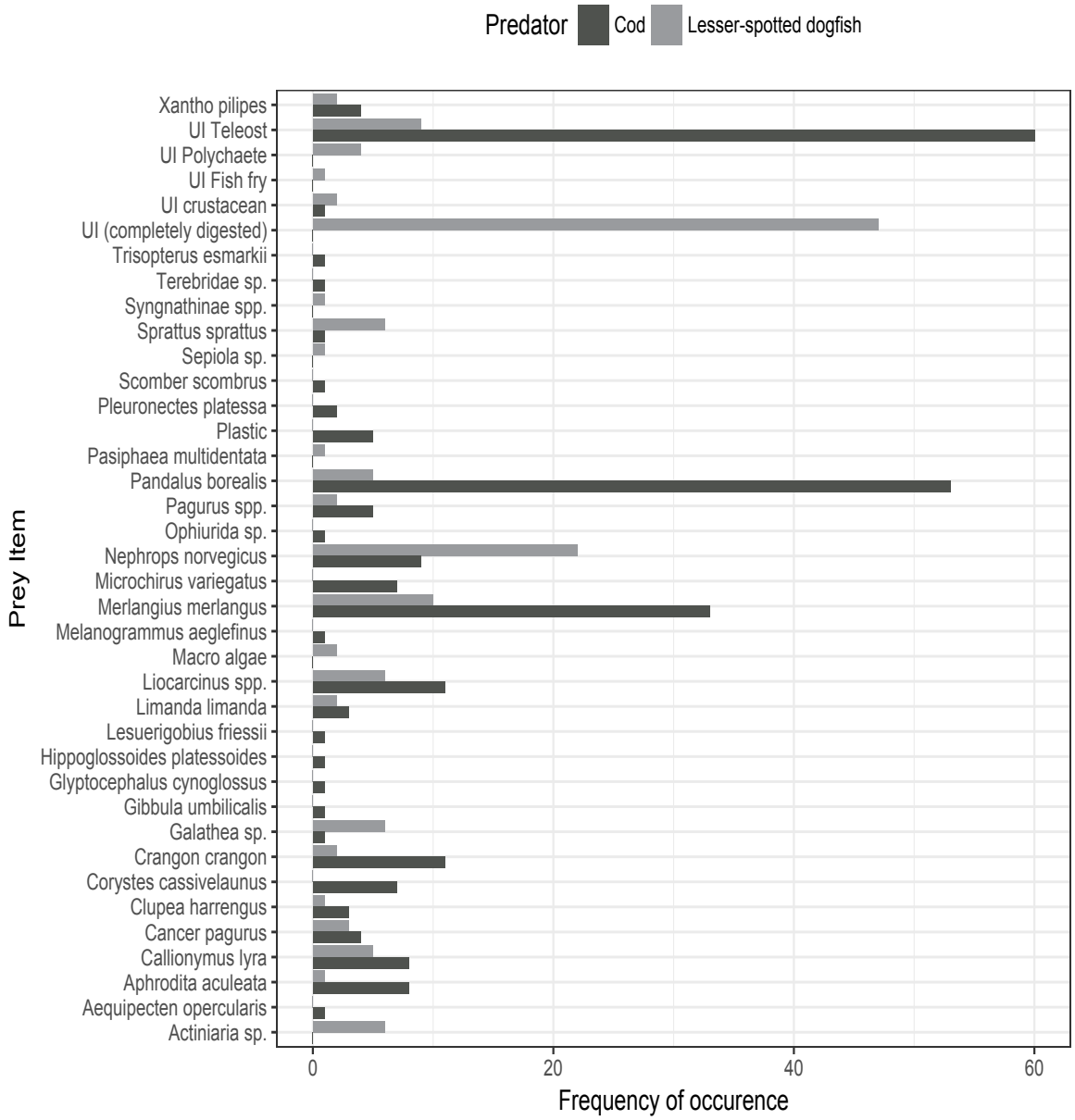


Fig. 4.4 Frequency of occurrence of prey items in predator gut contents

Stomachs with prey in made up 75.4% (n=89) of the cod sample and 97.4% (n=76) of the dogfish sample. Cod stomach fullness states were (1) 24.5%, (2) 20.3%, (3) 18.6%, (4) 17.7%, (5) 17.7%, (6) 0.84% (Fig. 4.6). Dogfish stomach fullness states were (1) 2.5%, (2) 21.7%, (3) 38.4%, (4) 25.6%, (5) 11.5%, (6) 0% (Fig. 4.6). Cod caught on gravel had significantly fuller stomachs (I_F) than those caught on mud (GLM: $F_{3,114}=3.15$, $p<0.05$; Fig. 4.7). Dogfish caught on mud had significantly fuller stomachs (IF) than dogfish caught on mixed substrates (GLM: $F_{3,74}=3.53$, $p<0.01$; Fig. 4.7). There was a significant main effect of "Predator" on I_F (GLM: $F_{1,195}=16.96$, $p<0.001$), "Substrate" had a non-significant main effect, and there was a significant interaction effect of "Substrate x Predator" (GLM: $F_{1,195}=5.57$, $p<0.001$; Fig. 4.7) where the mean I_F was significantly higher in lesser spotted dogfish than in cod caught on mud, and sand and silt substrates (Fig.4.7). There was no significant difference in I_F between sexes for cod or dogfish.

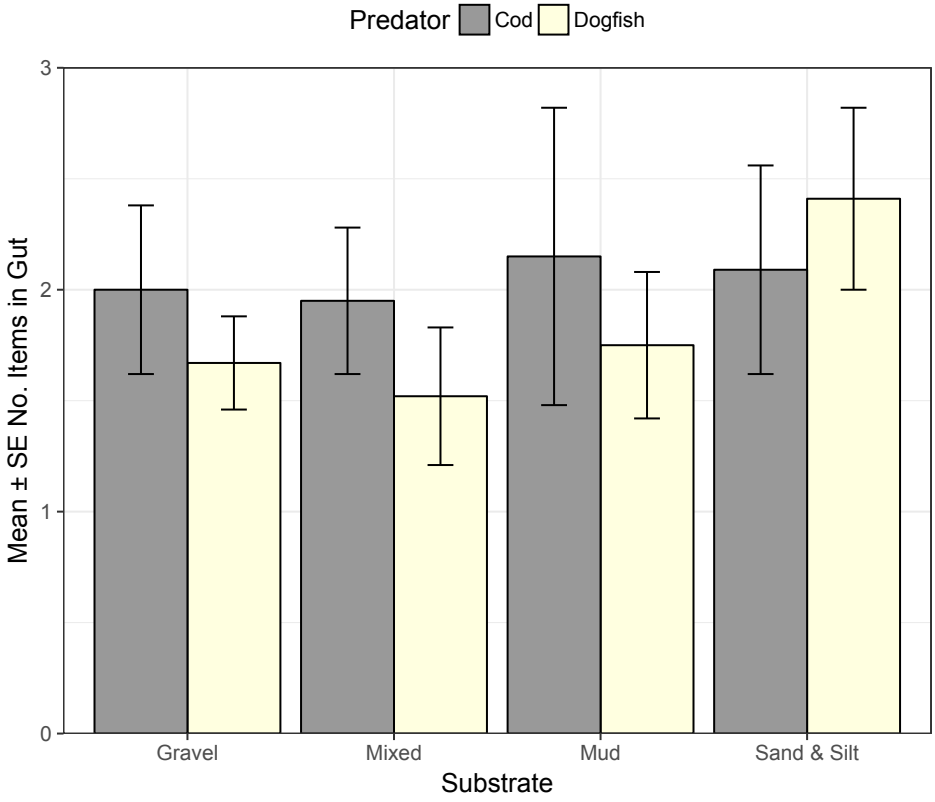


Fig. 4.5 Mean ± SE no. of items in predator gut contents on each substrate

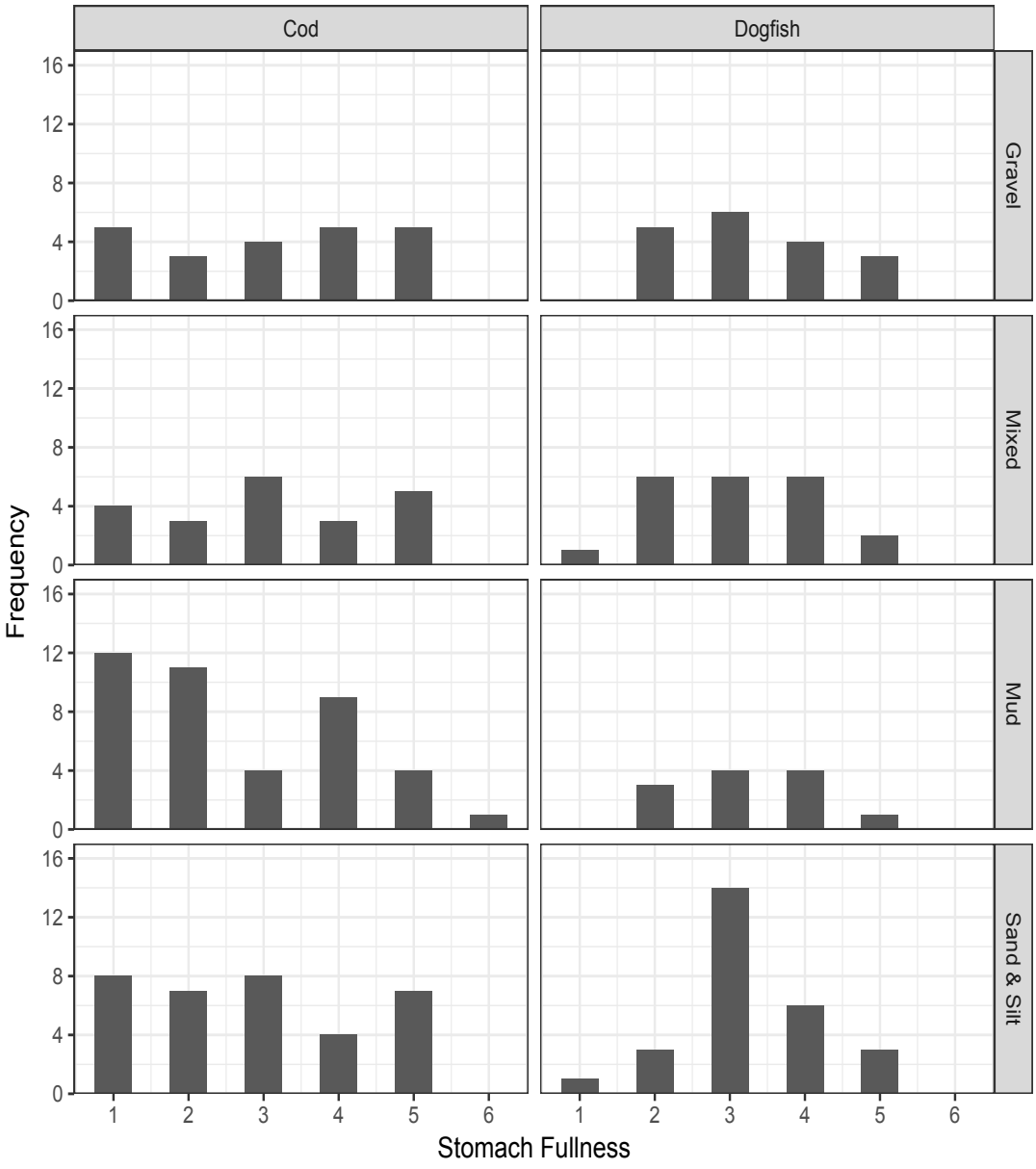


Fig. 4.6 Frequency of predator stomachs at each fullness state (1-6) on each substrate

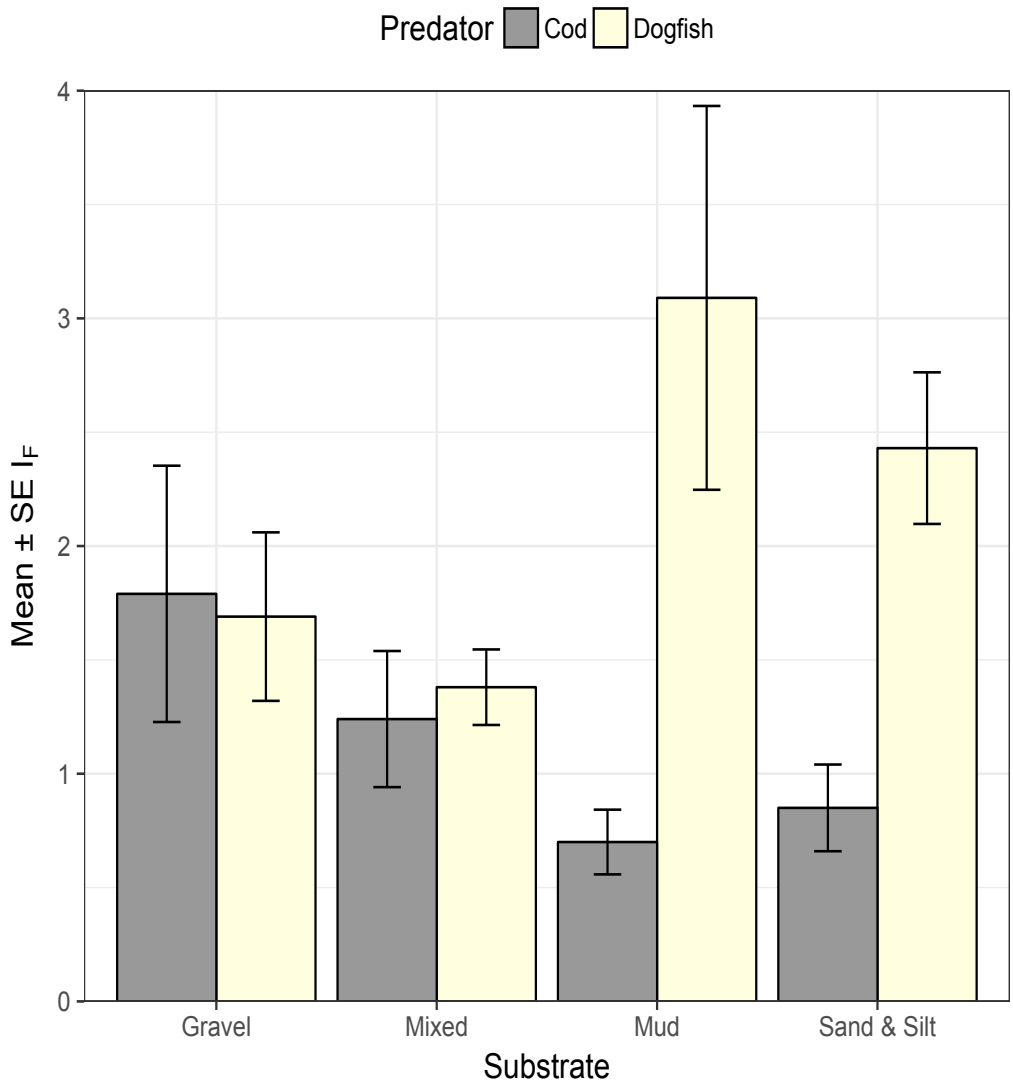


Fig. 4.7 Mean ± SE I_F predator gut contents on each substrate

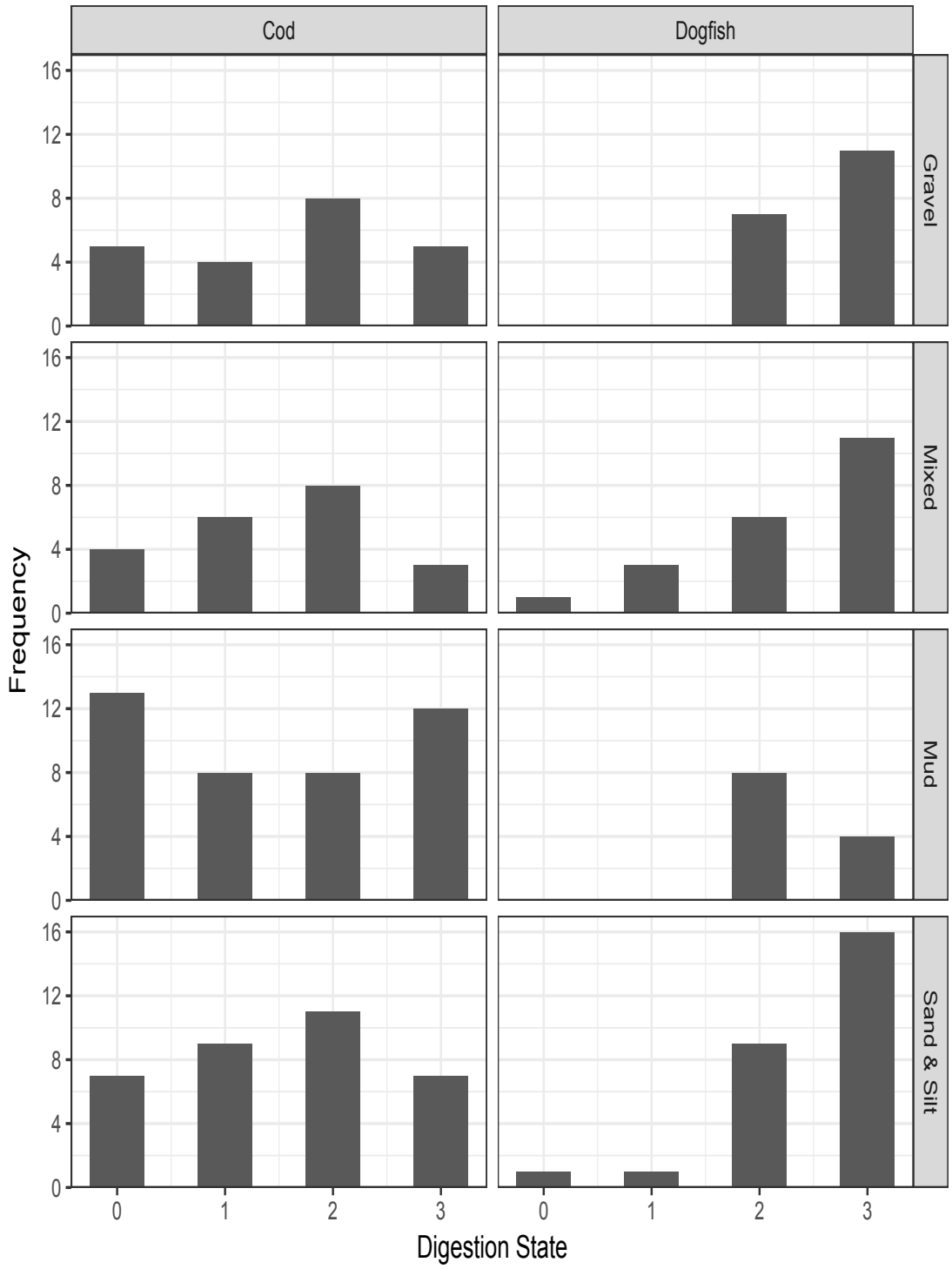


Fig. 4.8 Frequency of predator stomachs at each digestion state (0-3) on each substrate

Cod stomach digestion states were (0) 24.5%, (1) 22.8%, (2) 29.6%, (3) 22.8%. Dogfish stomach digestion states were (0) 2.5%, (1) 5.1%, (2) 38.4%, (3) 53.8%. Cod had a range of digestion states across each substrate but sand and silt has the highest occurrence of recently ingested food (Fig. 4.8). Dogfish gut contents were predominantly in a state of high digestion, this held true for each substrate type (Fig. 4.8). Mixed substrate had the highest occurrence of recently ingested food in dogfish gut contents (Fig. 4.8).

The most important prey categories according to IRIi% for cod were: UI teleosts 55.27%, *Merlangius merlangus* 23.37%, *Pandalus borealis* 12.44%, *Crangon crangon* 1.33%, *Nephrops norvegicus* 1.21%, *Liocarcinus spp.* 1.21%, *Callionymus lyra* 1.15% and *Microchirus variegatus* 1.15% (Fig. 9). The most important prey categories for dogfish were *Nephrops norvegicus* 52.14%, *Merlangius merlangus* 13.25%, UI teleosts 13.21%, *Liocarcinus spp.* 13.23%, *Galathea sp.* 3.13%, *Sprattus sprattus* 2.85% and *Actiniaria sp.* 2.85% (Fig. 9). *Melanogrammus aeglefinus* and *Glyptocephalus cynoglossus* only occurred once each, both in cod stomachs giving them values of 0.05% and 0.06% IRI_i and 0.8% and 0.99% GII_i respectively (Fig. 4.9).

Shoener's Index of niche overlap D = 0.63 demonstrates a significant overlap in the diets of cod and dogfish in the Irish Sea.

There were significantly more *Nephrops norvegicus* found in dogfish gut contents than in cod (GLM: $F_{1, 194} = 9.52$, $p<0.01$, $t=3.16$, $p<0.01$; Fig. 4.10). There were significantly more *Nephrops norvegicus* found in gut contents of predators caught on mud substrates (GLM: $F_{1, 191} = 3.10$, $p<0.01$, $t=2.11$, $p<0.05$; Fig. 4.10). There was no significant interaction between predator and substrate (GLM: $F_{3, 190} =0.79$, $p=0.37$) or between predator and sex (GLM: $F_{1, 186} =0.01$, $p=0.89$) on the number of *Nephrops norvegicus* found in predator gut contents.

There were no significant differences between the percentage abundance of commercial fish, commercial invertebrates, non-commercial fish and non-commercial invertebrates found in cod and dogfish gut contents (GLM: $F_{1,146}=0.49$, $p=0.48$; Fig. 4.11, Fig. 4.12). There were no significant differences between the percentage abundance of commercial fish, commercial invertebrates, non-commercial fish and non-commercial invertebrates in predator gut contents and substrates (GLM: $F_{3,140}=0.64$, $p=0.59$; Fig. 4.11, Fig. 4.12).

There were significant differences between the S-H values (GLM: $F_{2,48}$=13.03, p<0.001; Table 4.1, Fig. 4.13), post-hoc showed cod gut contents were significantly more diverse than dogfish gut contents (z=2.44, p<0.05; Table 4.1, Fig. 4.13), the environment was significantly more diverse than cod gut contents (z=2.27, p<0.05; Table 4.1, Fig. 4.13), and dogfish gut contents (z=4.81, p<0.001; Table 4.1, Fig. 4.13). There were no significant differences in diversity between substrates for cod and dogfish gut contents and the environment (Table 4.1, Fig. 4.13).

Table 4.1 Shannon Index H value for each station and predator gut contents

Substrate	Station	S H value: Environment	S H value: Cod	S H value: Lesser-spotted dogfish
Mud	17	2.33	1.72	0.56
Mixed	35	2.33	-	0.00
Mud	75	1.99	-	1.05
Mixed	86	1.45	1.50	1.52
Mixed	83	1.59	1.51	0.68
Mixed	81	1.58	0.95	0.00
Mud	101	2.36	0.68	0.45
Gravel	245	1.77	-	1.73
Sand and Silt	246	1.94	-	1.91
Gravel	77	1.97	0.33	1.33
Gravel	102	1.77	1.10	0.69
Gravel	243	2.27	1.63	0.00
Sand and Silt	345	2.19	1.76	0.00
Sand and Silt	259	1.85	1.33	1.63
Sand and Silt	258	1.75	1.33	0.00
Sand and Silt	256	1.63	1.77	1.67
Mixed	107	2.11	-	0.00
Mud	90	0.28	1.39	-
Gravel	63	1.48	0.94	-
Sand and Silt	100	2.33	-	-
	Total	36.98	17.92	13.24
	Mean	1.85	1.28	0.78
	Standard Deviation	0.48	0.43	0.73
	Standard Error	0.11	0.12	0.18

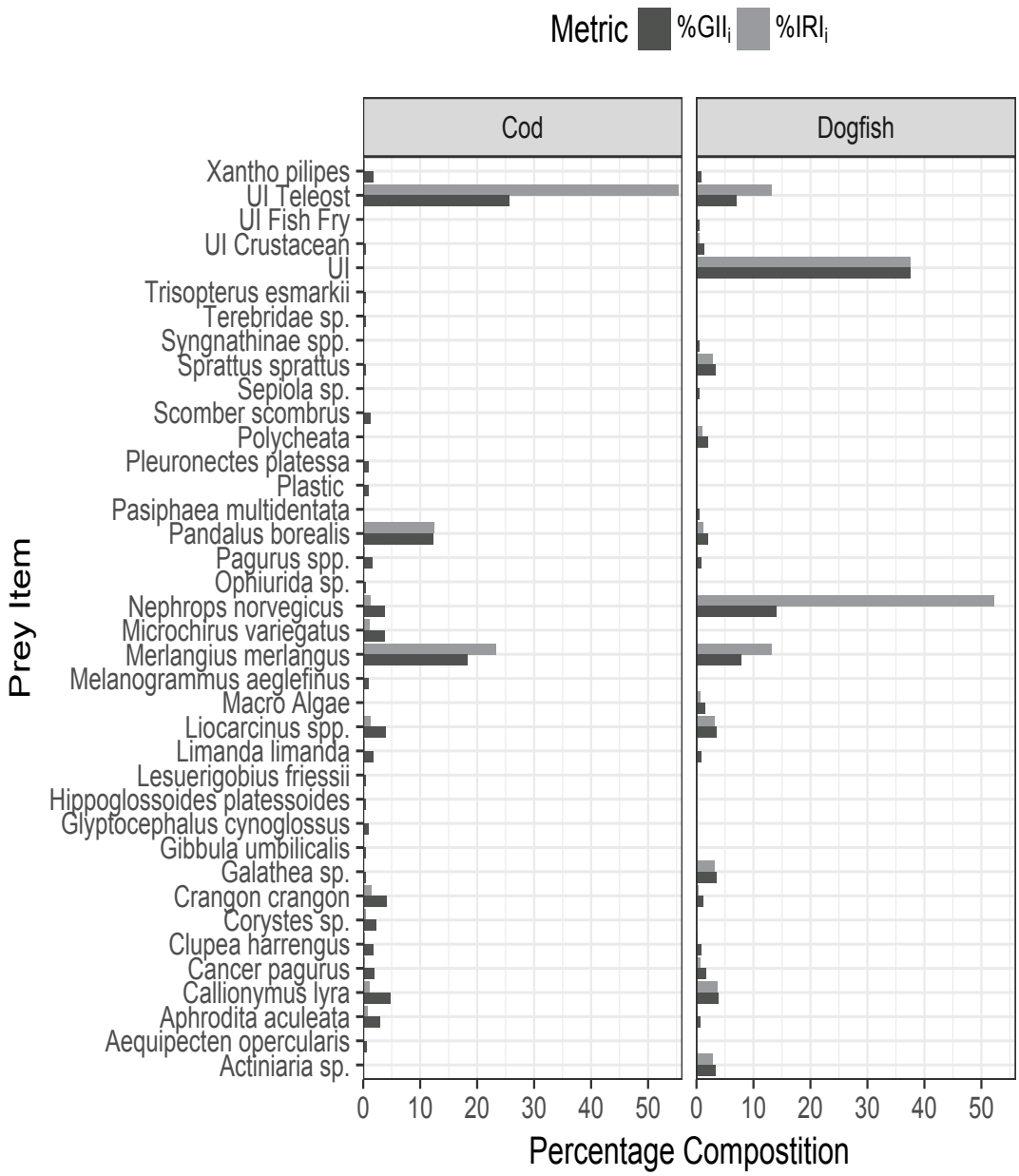


Fig. 4.9 Percentage composition of prey items in cod and dogfish gut contents

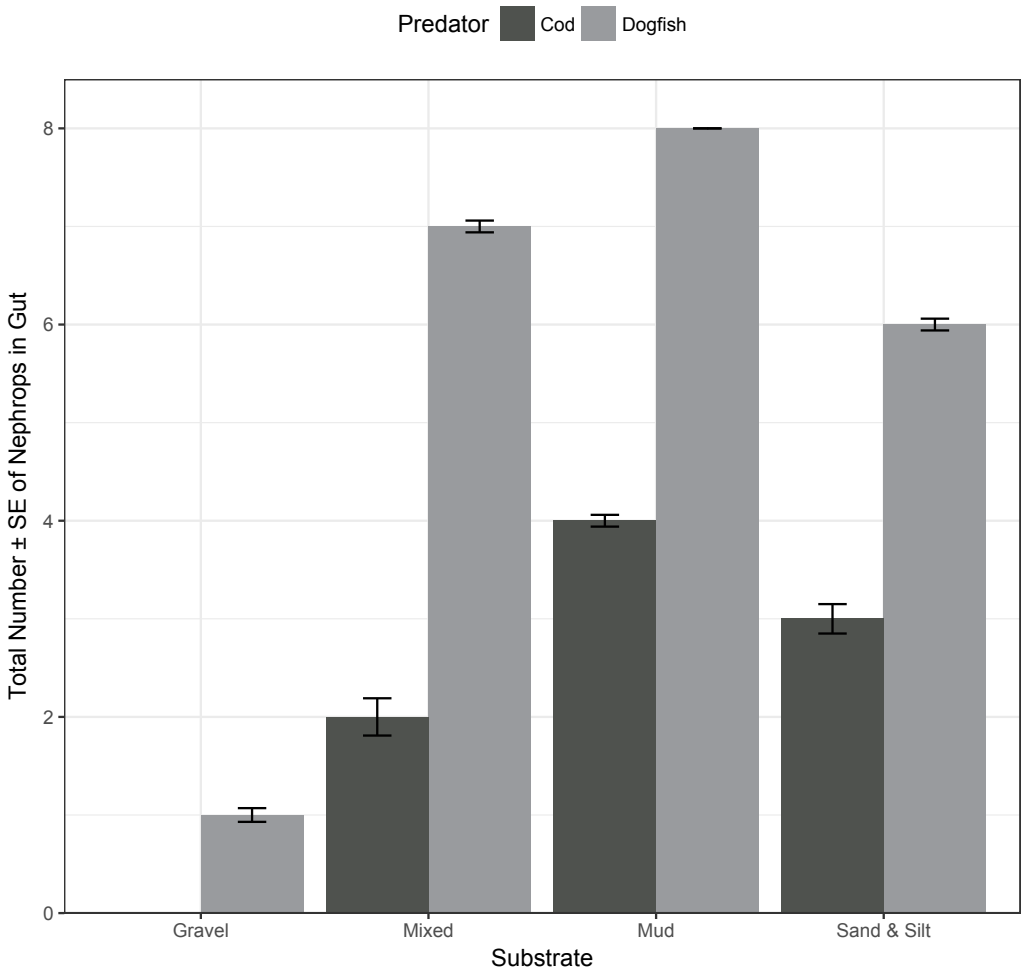


Fig. 4.10 Number ± SE of *Nephrops norvegicus* in predator gut contents on each substrate

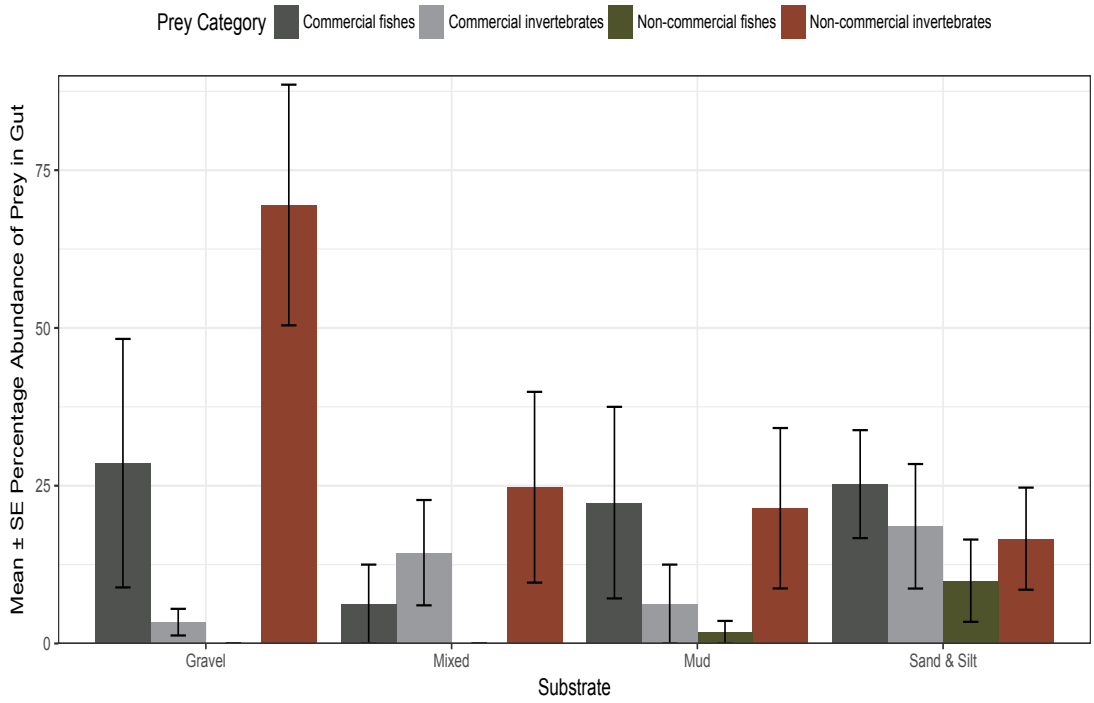


Fig. 4.11 Mean ± SE percentage abundance of prey category on each substrate in cod gut contents

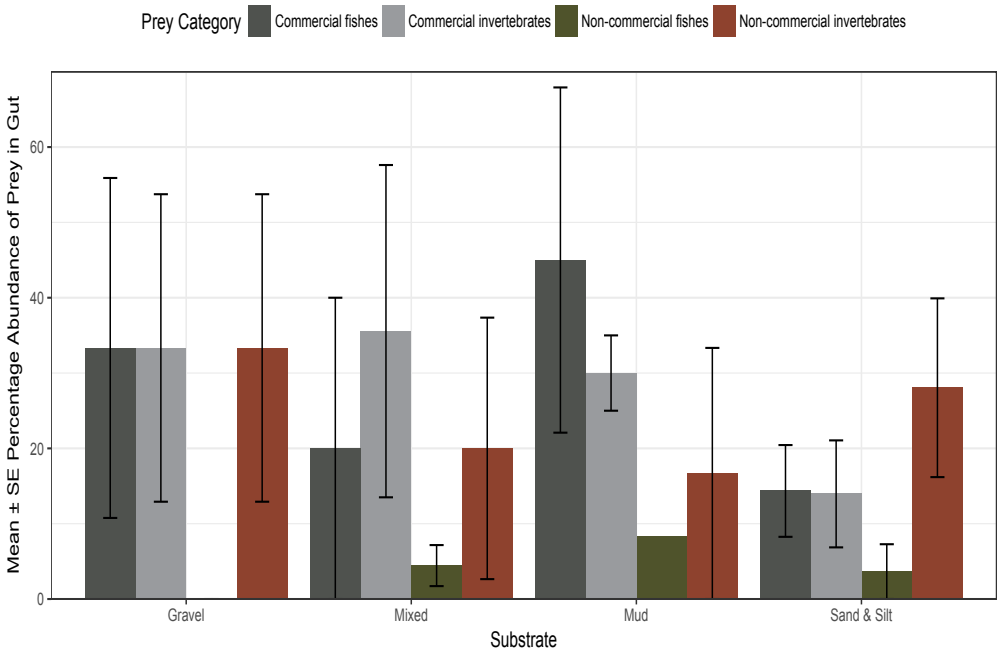


Fig. 4.12 Mean ± SE percentage abundance of prey category on each substrate in dogfish gut contents

There was no significant difference in prey selectivity overall, between cod and dogfish (t=1.41, df=62, p=0.16). Mean selectivity per Ivlev's index for cod was -0.5±0.12 and dogfish was -0.2±0.15 (Fig. 14). Cod actively selected for *Microchirus variegatus*, *Ophuirida sp.*, *Leseurigobius friessii*, *Terebridae sp.*, *Xantho pilipes* and *Gibbula umbilicalis* (Fig. 14). Dogfish actively selected for *Nephrops*, *Callionymus lyra*, *Actinaria sp.*, *Cancer pagurus, Pagarus spp.*, *Sepiola sp.*, *Terebridae sp.*, *Xantho pilipes*, and *Sygnathinae spp.* (Fig. 14). *Aphrodita aculeata* and *Pandalus borealis* were also actively selected for but they were not significantly selected for.

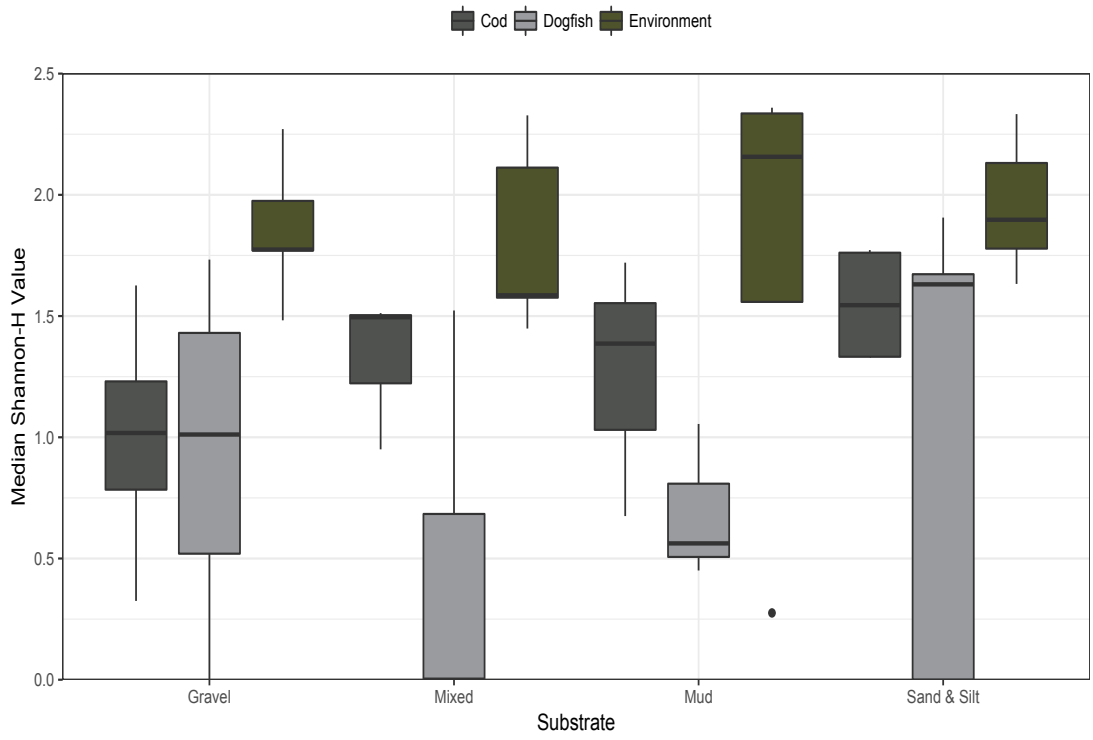


Fig. 4.13 Median Shannon-H value for predator gut contents and environment on each substrate

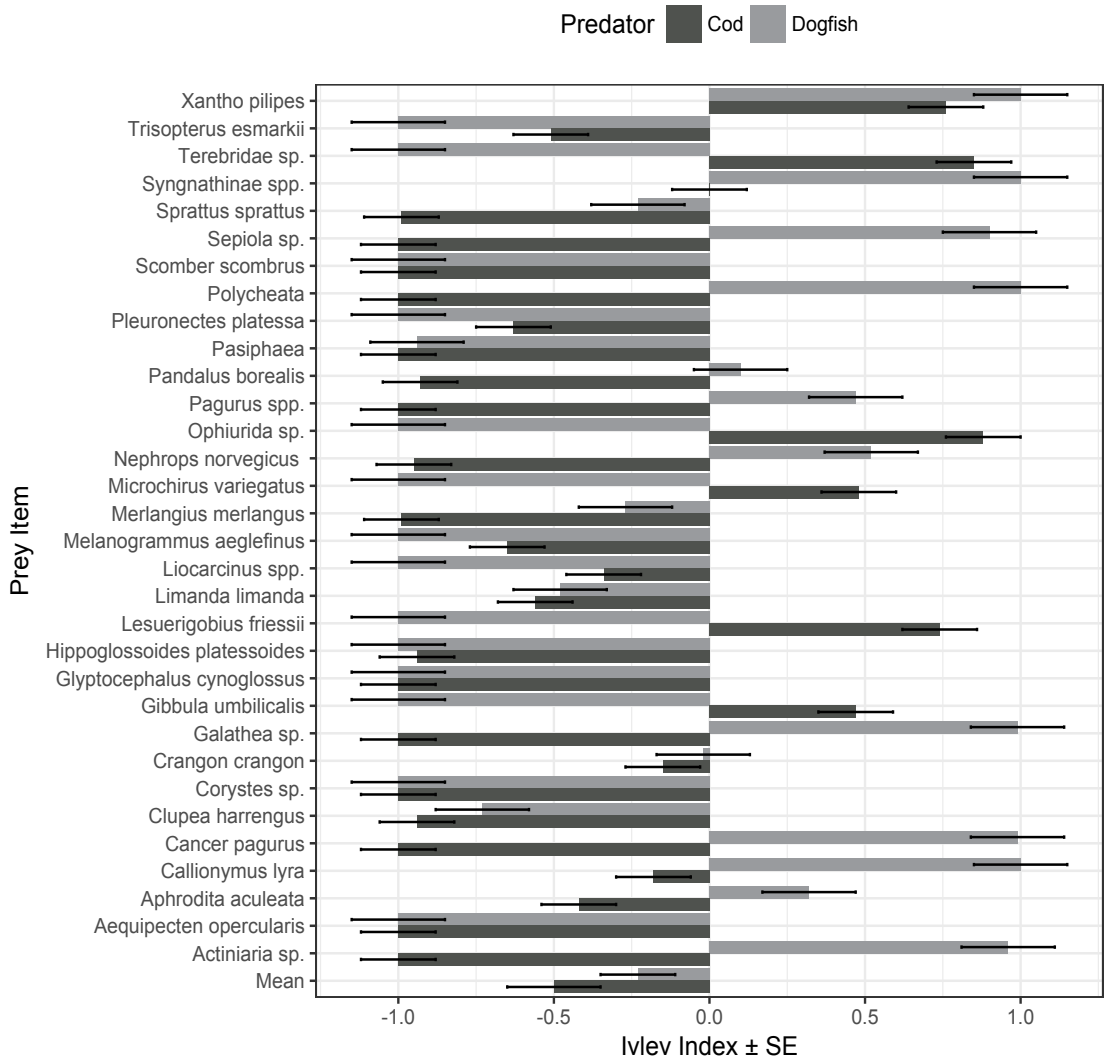


Fig. 4.14 Ivlev's Index ± SE of selection for the mean and each prey item found in cod and dogfish gut contents

4.4 Discussion

The data presented here maintains that cod and dogfish are both important generalist predators in the Irish Sea. Cod are part of a highly exploited fishery (Myers *et al.* 1996; Myers 1997; Katz *et al*. 2009) and have been subjected to a climate forced range shift (Walther *et al*. 2002; Cheung *et al*. 2009). This has elicited a reduction in population size and length classes which in turn limits the size of the yearly cohorts and reproductive capacity of the Irish Sea cod population (Richardson 2016). Contrastingly, there is a large and growing population of dogfish in the Irish Sea (Sguotti *et al.* 2016).

The substrate patches observed should not be considered as discrete areas due to connectivity and movement between the different strata. Cod did not exhibit significant selection for different habitat types however; a higher survival rate for young cod has been noted in high complexity substrates of rocky reef and cobble, hypothesized to be because of the high degree of refugia conferred (Gotceitas *et al.* 1995; Tupper & Boutilier 1995). More productive habitats allow a higher degree of growth in juvenile cod due to the abundant resources. Therefore there is a trade-off between predator avoidance and resource consumption (Gotceitas *et al.* 1995, Tupper & Boutilier 1995). Associations to substrates have been seen to change dependent upon individual age (Cote *et al*. 2004), temporal variations (Keats 1990; Cote *et al*. 2004) and density dependent utilization of other preferable substrates (Laurel *et al*. 2004). Furthermore, temperature changes may mediate the selection of particular substrate types in a trade-off for food availability and refuge versus physiological requirements (Freitas *et al*. 2016). My results presented in regard to substrate types should thus be taken as relative differences between habitat types, and caveated with the possibility of many other unmeasured variables coming into play.

Behavioural energetics dictate that individuals ought to select for the habitat with the highest net energy value, however while not specifically investigated during this study, habitat selectivity varies between male and female dogfish (Klimley 1987; Economakis & Lobel 1998; Sims 2003). Aggregations of elasmobranch species are a direct result of resource availability rather than the consequences of social behaviour (Hulbert *et al*. 2005; Jacoby *et al*. 2010). Thermoregulation is recognised as a strong driver for home range size and behaviour (White *et al*. 2007) and aggregating behaviours, such as that seen in dogfish could be

attributed to attempts to reduce energetic costs (Sims *et al*. 2006; White *et al*. 2007). There were significantly more dogfish caught on gravel substrates which are located around the Isle of Man, where the surrounding waters are 50-100m deep due to a deep trough to the west of the island (Kennington & Hisscott 2013). Aggregations may occur here due to the thermocline created by the trough and gyre and the proximity of abundant prey (Sims *et al*. 2001).

Cod are generalist predators that use suction feeding to capture prey (Brawm 1969), this mode of feeding means that prey are ingested whole which made semi-digested food easier to identify unlike the gut contents of dogfish. Cod feed at their lowest during January – March (Armstrong 1982) which means that the data reported here will be indicative of the lower bounds of cod feeding. As temperature increases during the summer months there is a higher feeding rate as an increase in temperature accelerates digestion rates (Armstrong 1982). Worm and Myers (2003) identified and used *Pandalus borealis* as a key species in cod diets due to its prevalence in gut contents on both sides of the Atlantic. Crustaceans are a more important component in the diets of juvenile cod than adults; *Pandalus* makes up 20% of diet in Arctic cod stocks (Mehl 1986) a value that is reflected in the data from the Irish Sea, a decrease in stomach weight and shrimp occurrence occurred as a function of prey reduction due to an increase in crustacean fishing pressure (Mehl 1986).

Whiting was the most important fish species in both cod and dogfish stomachs. Whiting has been found to make up 50% volume of diet of dogfish (Lyle 1983). Dogfish are opportunistic, generalist predators (Lyle 1983) in the Irish Sea, which feed throughout the day (Olaso *et al*. 1998). They are known to consume benthic and demersal prey alongside pelagic teleosts when abundant (Lyle 1983, Cortés 1999). Individuals over 17cm feed on whiting all year round (Olaso *et al* 1998), it was also the most abundant species found in the environment. Moreover, the length range of whiting found in stomach contents of dogfish correlates to that of the fisheries discard range (Olaso *et al*. 1998), it can be concluded that the concurrence of whiting fisheries and dogfish populations acts to reinforce population stability of dogfish due to the number of discards while effectively depleting prey populations (Olaso *et al*. 1998). This highlights the importance of commercial fishing activities on structuring local populations and the trophic interactions within. While I do not have data on fishing pressure in the area during

the survey, a study by Kaiser & Spencer (1994) dogfish gut weights did not increase after trawling, however, *Pandalus* and *Crangon* were only found in guts after trawling. *Pandalus* and *Crangon* are mobile scavengers that may be attracted towards disturbed areas due to discards and exposed resources, which in turn makes them more prone to predation. Similarly, to the present study, they found a high emphasis of crustacean and common dragonets in dogfish diets (Kaiser & Spencer 1994). Elasmobranch predators aggregated to the discarded area and the overall catch diversity increased after hauling and discarding (Olaso *et al*. 2002). Lesser spotted dogfish exploited the squat lobster discards but only blue whiting had a shift in diet composition, which increased in crustacean occurrence (Olaso *et al*. 2002). The discarded species made up 3-4 times more percentage frequency of occurrence than other prey species insinuating the importance of discard processes in the diets of predatory fish (Olaso *et al*. 2002). Due to dogfish high discard survival rate, they are able to substantially exploit the other discarded species (Olaso *et al*. 2002; Revill *et al.* 2005; Rogriguez-Cabello *et al.* 2005). Thus, it would be appropriate to acknowledge the importance of trawling activity by fishing boats and the survey boat on our data and on the current diets of predators in the Irish Sea.

Stomach fullness mediates the need to consume resources (Fletcher 1984; Gill 2003) therefore; stomach fullness and satiation levels control the rate of resource consumption but also selectivity (Gill & Hart 1994). If one prey species is more easily captured than another, this influences attack choices (Savitz & Jansson 1982) thus when there is simultaneous prey encounter switching behaviours may become apparent (Gill 2003). The benefit of prey consumption is a value which is apt to change depending on the motivational state of the consumer (Stephens & Krebs 1986; Hart & Ison 1991; van Baalen *et al*. 2001; Gill 2003). Food intake depends on the available space in the stomach (Sims & Davies 1994). Gastric evacuation is an important regulator for appetite return wherein the degree of stomach wall distention could stimulate physiological mechanisms (Jobling 1981; Grove 1986). Furthermore, this has implications not only for prey populations but also predator dynamics as when they are hungry they are more risk prone and less selective as they must reach their daily energetic requirement (Gill & Hart 1994). This confers a higher vulnerability to predation and fishing pressure (Cuthill & Houston 1997). There are also certain abiotic perturbations to endocrine activity such as temperature and oxygen concentration (Brett & Groves 1979).

Most cod stomachs that held prey were in a very formative stage of digestion, which suggests that they were recently ingested. This may be due to cod feeding on smaller fish and crustaceans while in the net, thus introducing bias into the actual prevalence of certain species in cod diet. Smaller cod have a faster digestion time (Daan 1973) therefore, if smaller cod were sampled there may have been evidence of more prey in highly digested states. The high proportion of crustacean species found in gut contents may be attributed to longer digestion and gastric evacuation times (Singh-Renton & Bromley 1996). In the study by Michalsen *et al*. (2008) female cod had a lower proportion of empty stomachs and were fuller compared to males. This is due to building up a quantity of energy reserves for breeding season as feeding is reduced at this time, and the females need to consume more than males to support a faster growth rate and larger size (Ajiad & Gjøsæter 1990; Michalsen *et al*. 2008).

Lesser spotted dogfish exhibit a constant feeding rate, which is balanced by gastric expulsion of the same rate (Sims & Davies 1994), wherein smaller meals are evacuated faster than larger meals (Macpherson *et al*. 1989). Nevertheless, the oxygen consumption of dogfish increases after a predation event (Sims & Davies 1994) which gives worrying implications in climate change scenarios involving increasing temperature and decreasing oxygen concentration. A high prevalence of empty stomachs in shark species has been correlated to a highly efficient digestive state brought on by short periods of intense feeding preceding longer periods of lowered activity (Wetherbee *et al*. 1990; Wetherbee *et al.* 2004), however, a high percentage of dogfish stomachs were found with contents in them but over half of the stomachs were at an advanced stage of digestion. As cold-water species, dogfish exhibit intense feeding activity but complete digestion takes much longer than in other sharks. Van Slyke and White (1911) investigated the digestion of high protein meals in lesser spotted dogfish and found that high protein meals take 2-3 days to completely clear through the digestive system and that dogfish, as cold-blooded vertebrates, take 6 times longer to digest and absorb protein than warm blooded organisms. Furthermore, this study selected for mature or almost mature individuals (defined as >50cm, (Ellis & Shackley 1997; Ivory *et al*. 2005)) while juvenile lesser-spotted dogfish have double the rate of metabolism than adults (Sims & Davies 1994; Sims 1996), perhaps if smaller individuals were included in the analysis there would have been more empty stomachs present. Morphology of the jaw is a determinant of prey selection not only due to size but also shape and orientation, thus

facilitates the capture of certain prey items (Scharf *et al*. 2000). There is sexual dimorphism in jaw morphology as males have longer teeth and a narrower and longer mouth (Ellis & Shackley 1997), though Lyle (1983) found no difference in diet composition between male and female dogfish around the Isle of Man. Newborn and adult dogfish have the same jaw morphology but juvenile jaws are more viscoelastic (Fahle & Thomason 2008). Dogfish teeth are laterally inclined and serve to sever prey in two, this could facilitate feeding on prey that are too large for their gape (Wilga & Motta 1998). Southall and Sims (2003) observed a novel method of feeding in dogfish whereby, the shark holds prey near the tail area using its dermal denticles and uses biting and tearing movements to feed. Southall and Sims (2003) hypothesised that this is an important feeding method as it allows for a larger dietary scope and therefore an increased potential for growth. This feeding mode reduces handling time (Gill 2003) and thus presumably digestion rate due to increased surface area, which could explain the frequency of advanced digestion states found.

Productive habitats are selected due to containing a higher quality of prey, therefore supporting energetic trade-offs (Sims 2003). Foraging decisions are made without aprioi knowledge of overall resource availability (Lessells 1995). Muddy substrates held the most diversity in the environment yet both species consumed the most diversity of prey on sand and silt substrates. Sand and silt substrates held the greatest percentage abundance of commercial fish prey and mud had the most for commercial invertebrate prey. Commercial invertebrates were actively selected for by lesser spotted dogfish. The discrepancy between environmental diversity and diversity consumed on each substrate may be explained due to muddy strata being occupied primarily by commercial invertebrate prey in a homogenous environment which attracts higher aggregations of predatory fish, both commercial and non-commercial but cod and lesser spotted dogfish exploit the populations of abundant *Nephrops* which make burrows in muddy substrate (Chapman & Rice 1971; Armstrong *et al.* 1991). Commercial invertebrates were found in similar abundances on graveled stations and may have a lower handling time on gravel. Stomach fullness data supports this hypothesis, as cod were the fullest on gravel substrates but the least full on muddy substrates. Dogfish showed the opposite trend in fullness as they were the fullest on muddy substrates but least on gravel, however, there was not a significant difference between the substrates. However, this must be caveated with the ascertation that these analyses did not control for movement of predators between

substrates further than assessing digestion state.

Dogfish consumed significantly more *Nephrops* than cod, and female cod consumed significantly more *Nephrops* than male cod, which could suggest that this prey item holds more value to females than to males. When considering *Nephrops* as a prey, they are inflexible due to their hard carapace and long pincers; this produces a problem efficiently packing them into stomach space (Bromley 1991). *Nephrops* have historically been an important prey species for cod as 88% of predation on *Nephrops* in the Irish Sea is by cod (Symonds & Elson 1983; Brander & Bennet 1986). Armstrong (1982) found *Nephrops* in 20-40% of stomachs of cod in the North-West Irish Sea between 1982-1983, this made up 12-28% of the daily food intake, which in turn equates to 1.7-5.4 thousand tonnes per year. Nonetheless, a substantial amount of this occurrence could be credited to discard practices. Larger cod are more inclined to feed on *Nephrops*, as they are more able to handle larger prey (Armstrong 1982). The data in this Chapter considered only mature cod, nonetheless, the disparity in *Nephrops* occurrence in cod stomach contents could be related to the reduction in frequency of larger cod length classes (Baudron *et al*. 2014). *Nephrops* are a low-quality prey item for cod as it takes 4.6kg of *Nephrops* to produce 1kg of cod. This is attributed to the exoskeleton being hard to digest and of little nutritional value (Björnsson & Dombaxe 2004). When fed on a diet consisting purely of *Nephrops*, cod has a far slower growth and digestion rate compared to a fish diet with *Nephrops* remaining in the gut after 72 hours (Björnsson & Dombaxe 2004). Additionally, over a time period of two months, captive bred cod reduced their intake of *Nephrops* from 40% to 10% when offered a fish prey species simultaneously (Björnsson & Dombaxe 2004).

Considerations of prey selection must take into account tradeoffs between profitability and handling time (Gill & Hart 1994; Gill 2003). Profitability varies with prey type as defense mechanisms vary, therefore some pose risk of injury while some have a longer handling time (Tomida *et al*. 2012). There is a threshold size of prey due to gape morphology and claw avoidance, thus there is a hump shaped relation of profitability to prey size (Tomida *et al*. 2012). Thus, why larger individuals of both species are more likely to consume crustacean prey than small individuals as they are better equipped to handle hard to digest prey. However, the results in this Chapter do not account for length of predator due to the small sample size. These tradeoffs are some of the underlying mechanisms of prey switching

behaviour. Switching of prey occurs within different feeding modes and spatially variable areas (Murdoch *et al*. 1975; Chesson 1989). Rindorf *et al*. (2006) confirmed the presence of negative switching in North Sea cod; wherein, there is a decreasing preference of a prey species at increasing relative abundance. They attribute this to the density mediated behavioural changes of prey in predator dense areas, such that prey becomes less vulnerable as density increases. However, there is a similar bias in Rindorf *et al.* (2006), as there is in the present study, in that there is a bias in the surveying technique of prey assemblages due to animal size and net size.

There are numerous inherent issues in the methodology associated with feeding and diet in in sitú investigations, but without these, laboratory experiments remain theoretical without relevant context (Strauss 1979). Kohler and Ney (1982) purport that data from in sitú feeding experiments should be construed as relative rather than absolute values. These problems are mainly associated with the accuracy of sampling invertebrate prey communities when the gear used is selective for fish species. Therein, selectivity indexes have a high degree of error associated with methods but also numerous quantifications of dietary composition (Bigg & Perez 1985; Cortés 1998). The present study employed numerous techniques to quantify predator diet in an attempt to reduce the inherent errors in single methodology (Liao *et al*. 2001). Due to different mechanisms of feeding, rate of digestion, and occurrence of either large or unusual prey in data sets, metrics can give ambiguous results (Hyslop 1980). Jacobs (1974) suggests that Ivlev's index is redundant when considering multiple different prey species with different relative abundances (see Kerr 1974; Platt & Denman 1978). When evaluating Ivlev's index, Strauss (1979) makes the point that reliability is a function of absolute and relative sample sizes, and the relative abundance of prey in the environment but finds a poignant issue in inadequate sampling techniques plus physiological considerations such as digestion rate confers a higher source of error. Schoener's Index is preferential for calculating niche overlap despite inherent issues (see Wallace 1981), this is supported by Linton *et al*. (1981) where Schoener's Index was the most accurate and held a constant level of error at very high and low estimates. The Geometric Index of Importance revealed similar results to the IRI_i; The slight differences between the IRI_i and GII_i reveal small-scale differentiation between the relative importance of prey categories where, instances in which the IRI_i results were the same, the GII_i appears more sensitive. Use of other technology available such as stable isotope analysis and baited camera

traps would allow a more refined view of trophic interactions and could be sampled across different temporal scales. However, both methods are very labour heavy and very expensive to carry out. Dietary data is often useful and used as a proxy it, however, the information gained from it is merely a snapshot of feeding patterns and thus should be considered within the context of quantifiable laboratory results.

Trophic interactions are a powerful driver of ecosystem stability (Paine 1980, Chapin *et al*. 1997; Winder & Schindler 2004; Canning & Death 2017) and the strength of consumer-resource interactions has the potential to stabilize or disrupt ecologically and economically important assets (Dick *et al*. 2014; Gellner & McCann 2016). Through the collation of diet data, it is possible to deliver rapid and low cost (as opposed to stable isotope analysis) information upon the feeding preferences and trophic interactions of predators in a system. The data presented highlights the differential feeding and exploitation of habitats by two predators. This is increasingly important to assess due to the movement of species ranges, and changing abiotic environment (Amarasekere 2015; Dick *et al*. 2017a,b; Uszko *et al*. 2017). Therefore, this is the first step to take before assessing changes in species interactions in the laboratory as survey data provides real world contextual relevance to the results achieved from laboratory work (See Chapter 5 & 6). This work highlights both predators as having substantial pressure upon commercial species, but when abundance is also taken into account, dogfish have a clear higher impact on prey species. This should be focused upon in further studies to assess how impact may change with predicted climatic change (Dick *et al*. 2017a,b; Laverty *et al*. 2017a,b; Uszko *et al*. 2017) (This will be addressed in Chapters 5 & 6).

Chapter 5

Effects of acute and chronic temperature changes on the functional responses of the dogfish Scyliorhinus canicula (Linnaeus, 1758) towards amphipod prey Echinogammarus marinus (Leach, 1815)

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5.1 Introduction

Temperature is a driver of interspecific interactions through mediating metabolism (Brown *et al*. 2004) and therefore locomotion (Dell *et al.* 2011; Dell *et al.* 2014), attack speed (Nowicki *et al*. 2012), feeding rates (Iacarella *et al*. 2015), and growth (Savage *et al*. 2004, Pörtner & Knust 2007). This has a direct effect upon energy flux through an ecosystem and the population dynamics within it (Woodward *et al*. 2010; Stevnbak *et al*. 2012; Cahill *et al*. 2013). Thermal responses are understood to be an underlying mechanism behind predator – prey dynamics (Berlow *et al*. 2009; Rall *et al*. 2010; Englund *et al*. 2011), but predicting the outcome of such interactions under future abiotic scenarios is highly problematic (Le Quesne & Pinnegar 2012). This is partly due to multiple layers of real world complexities such as habitat complexity (MacNeil *et al*. 2004; Ferner *et al*. 2009; Alexander *et al*. 2015; Barrios-O'Neill *et al*. 2015), light (Koski & Johnson 2002), multiple predator effects (Lang *et al*. 2012; Alexander *et al*. 2013; Wasserman *et al*. 2016a), but also due to the apparent species specificity of thermal dynamics (Lang *et al*. 2012). It is thus difficult to derive accurate conclusions from thermal responses modeled across numerous systems (Grigaltchik *et al*. 2012), but it is widely agreed that temperature change alters ecological stability (Dell *et al.* 2014; Gilbert *et al*. 2014).

Effects of temperature change can be discernable on an individual level (Huey *et al*. 1999; Calosi *et al*. 2013; Vasseur *et al*. 2014), and on population and community levels (Le Quesne & Pinnegar 2012; Rall *et al*. 2012). Furthermore, thermal change may manifest as long-term chronic temperature increase or as acute temperature variations over short periods of time (Vasseur *et al*. 2014). While chronic warming allows time for adaption to a higher temperature, short-term temperature variation exposes organisms rapidly to potentially adverse conditions. Both scenarios are caused by ongoing climate change (Easterling *et al*. 1997, 2000) and have the capability to affect the life history traits and fitness of organisms (Yocom & Edsall 1974; Biro *et al*. 2010; Terblanche *et al*. 2010; Clusella-Trullurs *et al*. 2011). Acclimation to temperature has been found to affect functional response parameters and cause unexpected differential changes in short-term interactions (Sentis *et al*. 2015). Therefore, taking differential responses of both predator and prey into account, and differential warming scenarios, needs to happen if reliable predictions are to be made (Sentis *et al*. 2015).

Warming oceans have the potential to alter interaction strengths between valuable commercial and non-commerical fisheries (Le Quesne & Pinnegar 2012). This has implications for maintaining biodiversity and economic value. As such there should be an emphasis on predicting and understanding the potential changes in species ecology under such climatic scenarios. This will pave the way for integrating results into management techniques well in advance so as to attempt to mititgate adverse change in community ecology and interaction strengths. I investigated predation by juvenile dogfish on amphipod prey (*E. marinus*). Both species are ubiquitous in temperate waters (Duffy & Harvilicz 2001; Froese & Pauly 2014), resilient (Múrias *et al*. 1996; Revill *et al*. 2005; Leite *et al*. 2014) and pliable laboratory species (Sims 2003). With regards to ecological relevance, *E. marinus* has large impacts upon community structuring (Duffy & Hay 2000; Dick *et al*. 2005), and is an important prey species (Leite *et al*. 2014) that can additionally be considered a proxy for other small crustacean species and small fish due to strong swimming behaviours. Dogfish are a generalist benthic predator (Kaiser & Spencer 1994; Domi *et al*. 2005) with high abundance (Genner *et al*. 2010; Sguotti *et al*. 2016), that has been found to increase with increasing temperature (Sguotti *et al*. 2016). Dogfish present as an ideal indicator species that is not affected by fishing mortality, due to lack of fishing pressure and high discard survival rate (Revill *et al*. 2005).

The present study presents the functional responses of dogfish preying on live *E. marinus* under the ambient temperature of 11±0.09°C and attempts to elucidate whether there is a change in the functional response when temperature is increased to 16.3±0.20°C, a value chosen as it is in line with future predictions (Solokov *et al*. 2009). I hypothesize that: (1) when the predator is acclimated, the maximum feeding rate of the dogfish increase above than of the ambient temperature; (2) when the prey is acclimated but the predator is not, the maximum feeding rate will be lower than when both predator and prey are acclimated. I attempt to use comparative functional responses to understand whether predator or prey was more profoundly affected by the temperature increase. A 2 x 2 factorial design was employed wherein both predator and prey were acclimated, just the predator was acclimated, just the prey were acclimated, and both predator and prey were unacclimated to 16.3°C.

5.2 Methods

Thirty captive bred juvenile dogfish (34.82±2.77SE) cm total length) were kept in three holding tanks (120 x 60 x 60 cm) at Queen's Marine Laboratory (QML Portaferry) and maintained on chopped mussel and mackerel *ad lib*. three times a week. Trials were carried out from May-June 2016. The holding tanks were supplied with 11°C UV filtered seawater pumped directly from Strangford Lough. *Echinogammarus marinus* were collected by searching under cobbles on 'Walter's Shore', Portaferry. These were kept in aerated 28l boxes. *Echinogammarus marinus* was fed with *Laminaria digitata* which was replaced once a week.

The experimental setup involved three leader tanks (120 x 60 x 60 cm) heated with aquarium heaters. Three flow through systems provided seawater into the leader tank to be heated, the water then flowed from the leader tank into six 60l arenas. Airlines were fed directly into each leader tank to avoid confounds of low dissolved oxygen concentration (kept above 70% saturation DO). Acclimation to the desired heat took place over 3 days as temperature was increased from ambient to 16.3°C at a rate of 2°C every two days, and then a further two days at 16.3°C. Ten lesser-spotted dogfish were in each leader tank during acclimation. *E. marinus* were acclimated in 28l boxes via the flow through system. The dogfish were fed *ad lib.* throughout to avoid hyperphagy (Wootton & Ali 2001, Ali *et al*. 2003). Once the desired temperature was achieved, the water was held at 16.3±0.20°C. Mean summer temperature in Strangford Lough is 15.5°C, therefore the temperature chosen reflects potential daily variation in the summer and the 3-5°C temperature increase predicted in the coming century (Solokov *et al*. 2009).

A 2 × 2 experiment design was implemented wherein Factor 1 was "Predator Treatment" with respect to non- acclimation/acclimation to increased temperature and Factor 2 was "Prey Treatment" with respect to non- acclimation/acclimation to increased temperature. Therefore, treatments were: "Predator Acclimated" (prey unacclimated), "Prey Acclimated" (predator un- acclimated), "Both Acclimated", "Both Unacclimated". An "Ambient" temperature treatment at 11 ± 0.09 °C was included to get a baseline comparison. This was the temperature of Strangford Lough during the trial period, it represents the current spring average (AFBI 2016). This was preferred to a winter average due to the very low temperatures in winter slowing feeding behaviour in preliminary trials. Lesser-spotted dogfish were selected at

random, measured and placed in arenas an hour before the trials started. Recovery time was short as the specimens were captive bred and somewhat used to handling. Densities of prey were supplied at 1, 3, 5, 10, 15, 20 (n = 4 per density); prey size was ~5– 10 mm. Trials lasted for 2 h and the number of prey consumed were recorded at the end of this time by an observer. Individual fish were then placed in ambient temperature holding tanks for a week before reuse, no fish was reused in the same treatment or at the same prey density to avoid pseudo-replication. Amphipods were kept in experimental arenas in the absence of predators at each density treatment (n = 3 per density).

5.2.1 Statistical Analyses

Data were non-parametrically bootstrapped (n=30) to calculate multiple estimates of attack rate, handling time and maximum feeding rate. Welch's t-test was used to test differences in bootstrapped parameters between "Ambient" and "Both acclimated" (i.e. "raised') groups. Generalised linear models (GLM) with quasi-Poisson error distribution, to account for over dispersion in the model, were used to test for differences in functional response parameters (a, h, $1/h$T) with respect to two factors, "Predator Treatment" and "Prey Treatment". Tukey honest significant difference post-hoc tests were used to generate multiple pairwise comparisons.

FRs were modelled used non-replacement prey supply models (Equations 1.1, 1.2, 1.3). Suitability of each model was compared with Akaike Information Criterion (ΔAIC). Functional responses were then fitted using maximum likelihood estimation (MLE; Bolker 2010) and the Lambert W function (Bolker 2008). In the case that the logistic regression and GLM were insignificant, LOWESS lines were used to visually inspect the proportional consumption of prey to determine FR type.

5.3 Results

Control group prey survival was >99% and thus prey mortality was assumed to be due to predation in the experimental groups. Attack rate was significantly higher at ambient (0.92±0.05 SE) than raised temperature (0.10±0.010 SE) ($t= 13.82$, $df=30.59$, $p<0.001$). Handling time was significantly shorter at raised temperature (0.06±0.008 SE) compared to ambient (0.10±0.008 SE) ($t= 4.18$, $df=51.03$, $p<0.001$). This translated into a significantly higher maximum feeding estimate at raised

temperature (29.42±4.23 SE) compared to ambient (12.37±1.67 SE) (t= 3.74, df=30.91, p<0.001).

5.3.1 Prey consumed

Overall, significantly more prey were consumed when the predator was acclimated as opposed to not acclimated ($F_{1, 92}$=5.68, p<0.05; Fig. 5.1a), but there was no effect of prey acclimation ($F_{1, 92}$=0.48, p=0.49; Fig. 5.1b) and no significant interaction ($F_{1, 92}$=0.22, p=0.63; Fig. 5.1c).

5.3.2 Attack rate

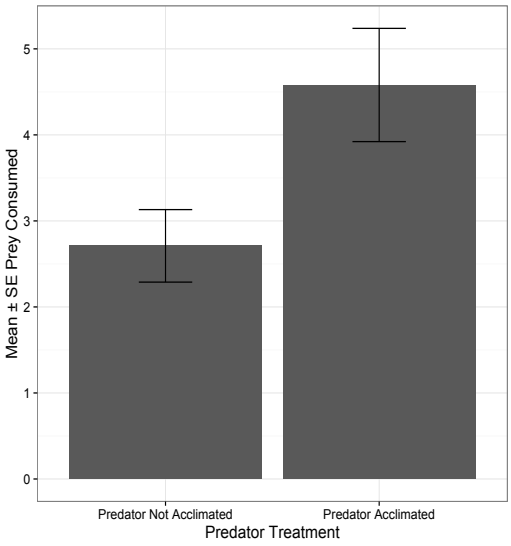
Attack rate had a significant "predator treatment" x "prey treatment" interaction effect ($F_{1, 102}$=98.69, p<0.001; Fig. 5.2c). Wherein, predators that were non-acclimated showed higher attack rates to prey that were acclimated as compared to prey that were non-acclimated, whereas predators that were acclimated showed higher attack rates toward non-acclimated as compared to acclimated prey (Fig. 5.2c)

5.3.3 Handling time

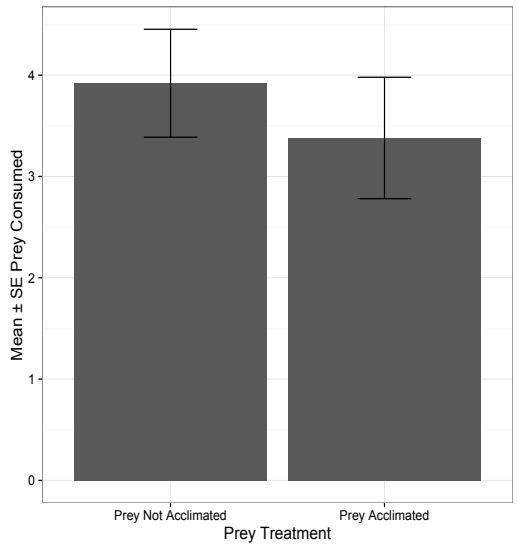
Handling time had a significant "predator treatment" x "prey treatment" interaction effect ($F_{1, 102}$=32.14, p<0.001; Fig. 5.3c). That is, predators that were non-acclimated showed higher handling time to prey that were acclimated as opposed to non-acclimated, and predators that were acclimated showed higher handling times to prey that were non-acclimated as opposed to acclimated (Fig. 5.3c).

5.3.4 Maximum feeding rate

Maximum feeding rate had a significant "predator treatment" x "prey treatment" interaction effect ($F_{1, 102}$=17.75, p<0.00; Fig. 5.4c). When predators were non-acclimated the maximum feeding rate was similar towards prey that were non-acclimated and prey that were acclimated, whereas when predators were acclimated the maximum feeding rate was higher towards prey that were acclimated as compared to non-acclimated prey (Fig. 5.4c).



a



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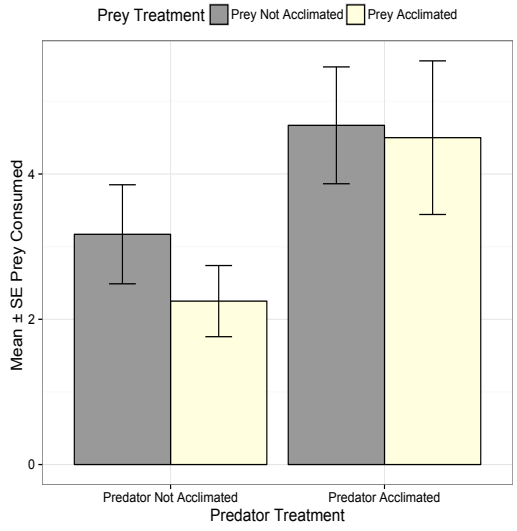


c

Fig. 5.1 Mean ± SE of number of prey consumed for **a**) predator treatment, **b**) prey treatment, and **c**) interaction of predator and prey treatments

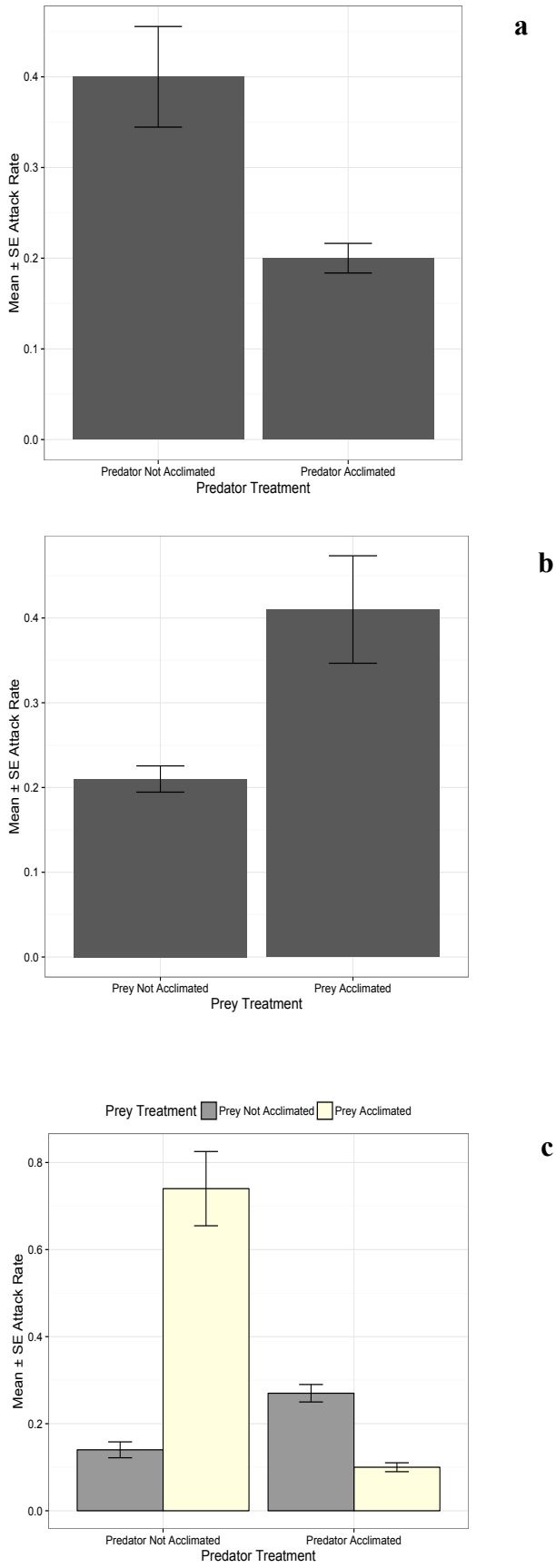


Fig. 5.2 Mean ± SE of bootstrapped attack rate for **a**) predator treatment, **b**) prey treatment, and **c**) interaction of predator and prey treatments

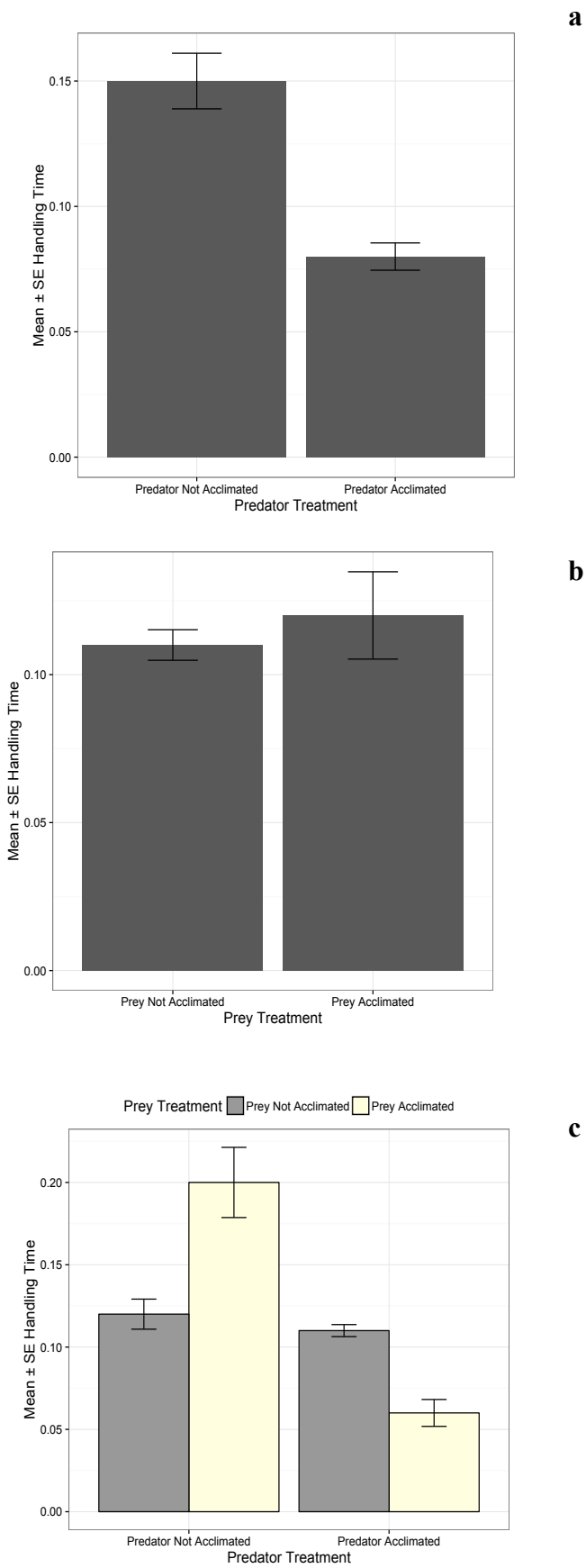
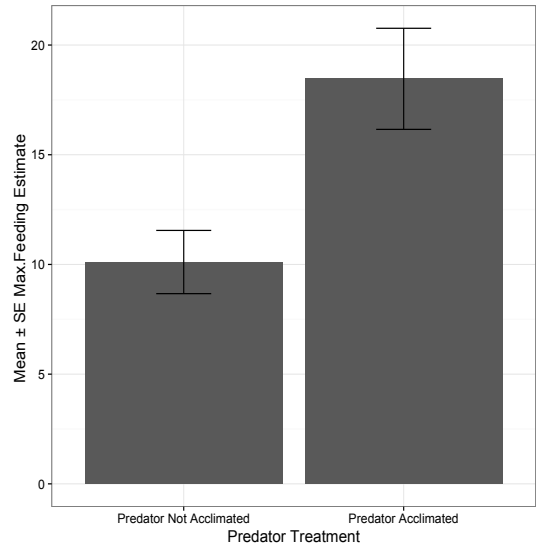
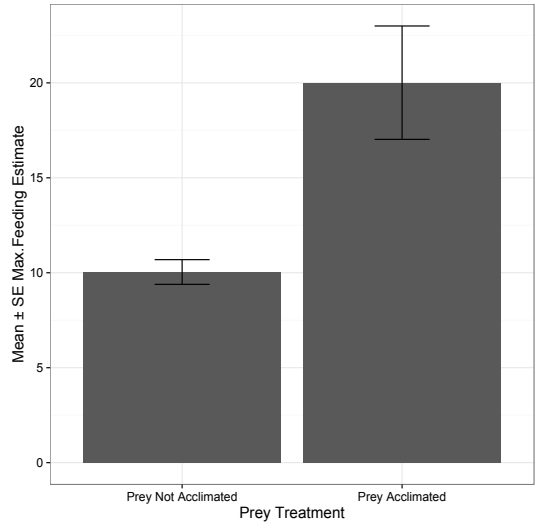


Fig. 5.3 Mean ± SE of number of bootstrapped handling time for **a**) predator treatment, **b**) prey treatment, and **c**) interaction of predator and prey treatments





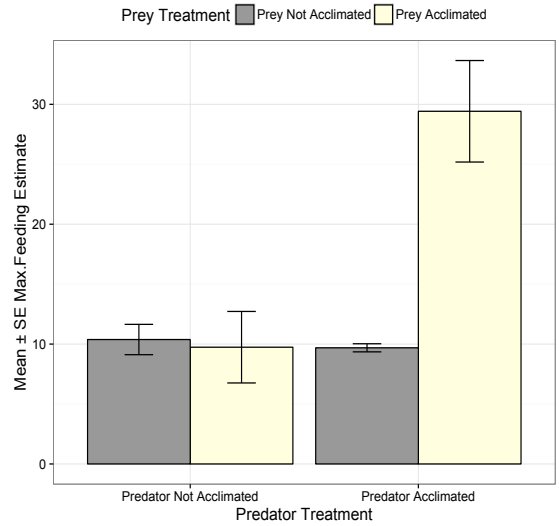


Fig. 5.4 Mean ± SE of bootstrapped maximum feeding estimate (hr^{-1}) for **a**) predator treatment, **b**) prey treatment, and **c**) interaction of predator and prey treatments

5.3.5 Functional Response

At ambient temperature (11°C), the predator showed a Type II functional response (Table 5.1, Fig. 5.5). When just the predator was acclimated to 16.3°C, there was no statistically significant Type III functional response, indicating that in this treatment there is a boundary Type I/Type III response. Therefore, while fitting the model of a Type I response at the densities investigates, it was modeled as a Type III (Jeschke *et al.* 2004) (Table 5.1, Fig. 5.5). When both predator and prey were acclimated to 16.3°C a Type III response was fitted to the data (Table 5.1, Fig. 5.5). This had the highest maximum feeding rate estimate. When just the prey was acclimated there was a Type II functional response (Table 5.1, Fig. 5.5). When both predator and prey were unacclimated to 16.3°C there was a non-significant Type III functional response which, again, was instead modeled as a Type III as suggested by the shape of the GLM (Table 5.1, Fig. 5.5). This has the lowest maximum feeding rate estimate. In both instances where there was a non-significant logistic regression and GLM, locally weighted scatterplot smoothing was used on the proportion of prey consumed per density to investigate the shape of the response (Fig. 5.6). It should be considered here that the handling times reported for predator acclimated and both unacclimated are unreliable due to the Type I response generated at the prey densities investigated.

Table 5.1 Functional response types, first order term from logistic regression, first and second order terms from GLM are reported with *p* values for all treatments

Treatment	(Log. Reg.) First order term, (*p*)	(GLM) First order term, (*p*)	(GLM) Second order term (*p*)	Functional Response Type
Ambient	-0.053, (<0.05)	-0.133, (0.25)	0.003, (0.47)	II
Predator Acclimated	-0.024, (0.30)	0.164, (0.14)	-0.007, (0.08)	III
Both Acclimated	0.087, (<0.001)	-0.127(<0.001)	0.008, (0.05)	III
Prey Acclimated	-0.025, (0.33)	-0.365, (<0.01)	0.014, (<0.01)	II
Both Unacclimated	0.008, (0.74)	0.071, (0.54)	-0.002, (0.58)	III

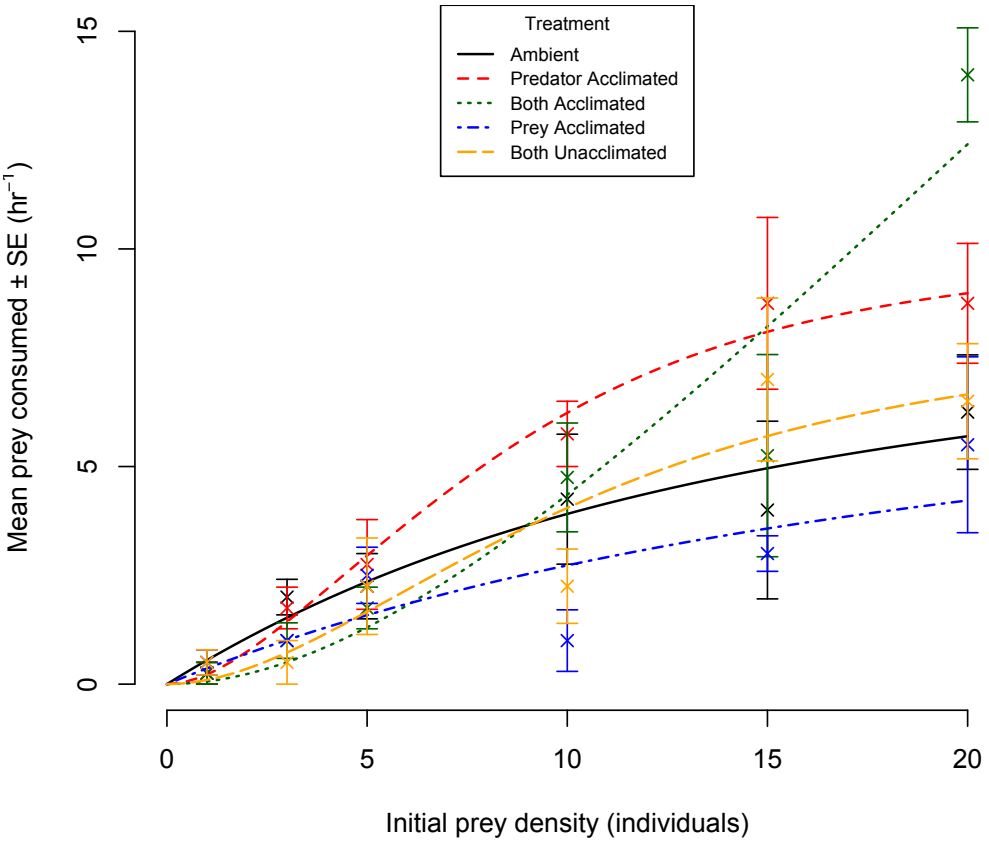


Fig. 5.5 Functional response curves of *Scyliorhinus canicula* on *Echinogammarus marinus* for all treatments with standard error bars from raw data

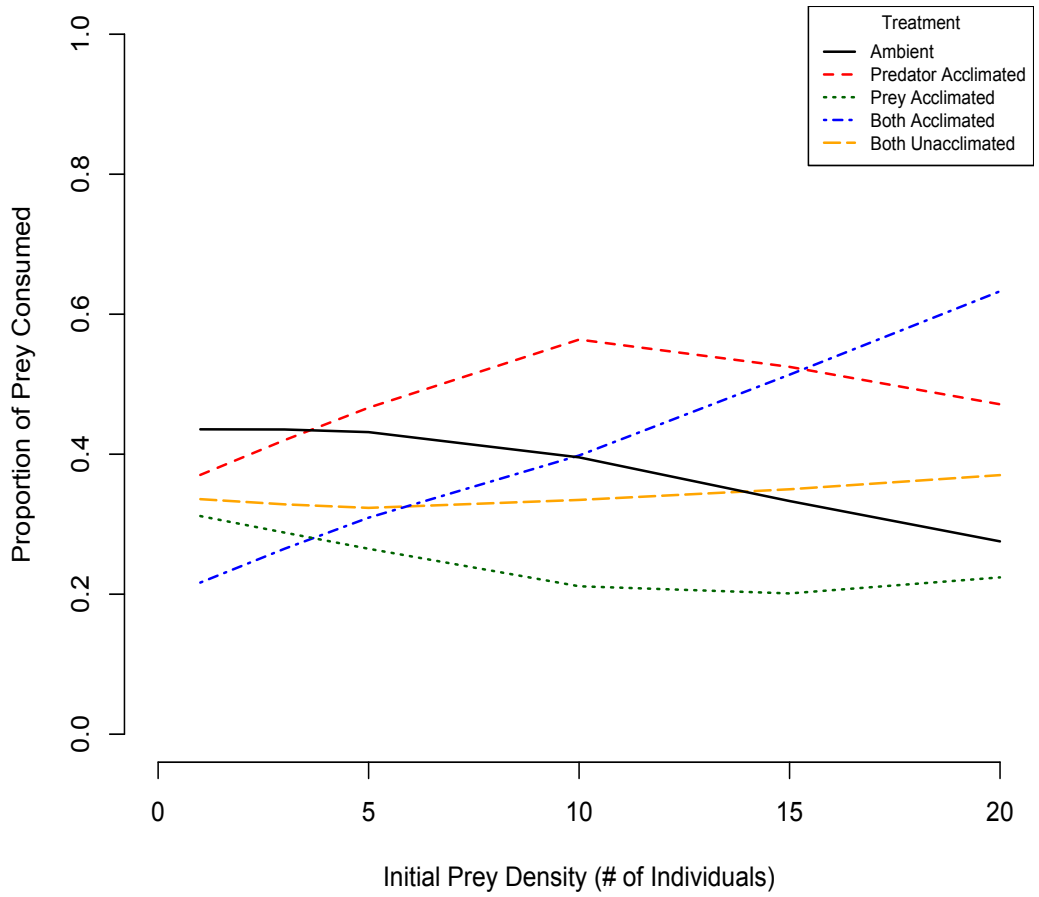


Fig. 5.6 LOWESS lines fitted to the proportion of prey consumed at each density per treatment

5.4 Discussion

Prediction of the ecological ramifications of facets of climate change is particularly difficult due to inherent confounds of interactions between dissolved oxygen concentration and temperature (Peck *et al*. 2009; Grigaltchik *et al*. 2012) and multi-species systems (Broitman *et al*. 2009). However, here I have shown that by using comparative functional response analyses, in a similar way to invasive species impact predictions (Dick *et al*. 2014; Wasserman *et al*. 2016b), it is possible to identify the impact of a predator under various warming scenarios and assess whether there are interaction effects when both sides of the predator-prey dynamic are considered.

There was no significant difference in the number of prey consumed at higher temperature than at ambient temperature, however the temperature increase mediated changes to the parameters associated with the functional response. Nonetheless, number of prey consumed is not a reliable indicator of predatory strength in this case due to the prey densities being allowed to deplete, thus attention should concentrate on the relative values of the parameters associated with feeding.

Temperature increase mediated changes to the parameters associated with the functional response. There was a significantly higher attack rate when at "Ambient" temperature compared to "Both Predator and Prey Acclimated" to 16.3°C. This contrasts with the meta-analysis by Rall *et al*. (2012) and the assumption that attack rate is temperature invariant (Dell *et al.* 2014), but is similar to results in Grigaltchik *et al*. (2012), wherein there was a decreased attack rate but a high predation pressure at increased temperature. Further, my results are similar to Wasserman *et al*. (2016b), wherein attack rate was highest in the lowest temperature at zero habitat complexity. Furthermore, attack rate considers both predator and prey responses thus, at a lower temperature, swimming speed may be decreased in the smaller bodied prey species and therefore make them easier to attack as they must use more energy to escape (Dell *et al.* 2011, 2014). As a consequence, the attack rate of the predator may be higher at lower temperature due to a change in attack success as a result of prey escape energy. The handling time was significantly shorter at the higher temperature and therefore the maximum feeding rate estimates were significantly higher at the higher temperature. Temperature directly affects poikilotherm metabolism and has a somewhat bell-shaped relationship with maximum consumption (Englund *et al*.

2011). At ambient temperature, dogfish take 2-3 days to fully digest a meal due to the slower rate of chemical reactions at low body temperature (Slyke & White 1911), thus the increase in digestion rate is comprehensible at a higher temperature (Gilbert *et al*. 2014). Juvenile lesser-spotted dogfish have almost double the metabolism rate of adult specimens (Sims 1996), so despite the short trial time, the predator may experience more motivational states during the raised temperature treatments due to the increased rate of digestion. This may alter searching behaviour at high prey densities (Clark & Mangel 2000; Ariyomo & Watt 2015). The behaviours that make up handling time are considered to be composite of a multitude of processes including; subduing, chewing, swallowing, digestion and gut evacuation, all of which are controlled by physiological processes that are affected in different manners by increasing temperatures (Jeschke *et al.* 2002). This produces a complex picture, wherein, the attack rate is high at low prey densities under current temperatures which could manifest as destabilising for prey populations. Warming may mitigate the risk for low density prey populations due to the change in Functional Response Type to the stabilising Type III under raised temperatures. Nonetheless, there was a higher maximum feeding rate at the raised temperature treatment which suggests that despite a change in resource consumption with regards to resource density, the end result remains that consumption increases due to temperature increase as a result of shorter handling time.

Attack rate signifies the instantaneous rate of successful search (Holling 1959) and determines the initial increase of consumption at low resource density. When the predator was non-acclimated the attack rate was higher towards acclimated prey. This may be due to the temperature rise increasing the metabolism of the prey and causing a consequent increase in prey velocity and increased boldness (van Baalen *et al*. 2001; Nowicki *et al*. 2012). As a result, more stimuli are provided to the predator and the encounter rate is increased, leading to a higher attack rate when the prey is acclimated (Curio 1976; Taylor 1984). However, when the predator was acclimated the attack rate was higher toward non-acclimated prey and lower toward prey that were acclimated. This suggests that acclimation to temperature may dampen attack rate in juvenile lesser-spotted dogfish and thus negate the effects of increased prey stimuli.

Handling time relates to the time taken to eat and digest prey items (Jeschke *et al.* 2002). Unfortunately, we cannot discuss the handling times of the treatments

"Predator Acclimated", and "Both Unacclimated" with conviction, due to the non-significant logistic regression and GLM first and second order terms. Nonetheless, I can speculate from the results accumulated that at higher prey densities there may be further differences in resource consumption and, thus, handling times, as the motivational state changes (Englund *et al*. 2011). When the predator was non-acclimated the handling time was longer towards prey that were acclimated. This demonstrates that prey acclimation to temperature has a large effect on the handling of the prey possibly due to a mis-match in swimming speed of predator and the prey, and digestion speed in the predator (Dell *et al.* 2011). When the predator was acclimated the handling time was longer towards prey that were non-acclimated. This may again be related back to encounter rate (Curio 1976; Taylor 1984) and an increased metabolism and digestion speed due to acclimation of the predator (Dell *et al.* 2011). Therefore, when predator and prey are both acclimated to the same temperature there is a decrease in handling time which implies that consumption rates will also increase with temperature warming. While the effects of oxygen concentration were not tested in the present study, air was bubbled through all arenas during the treatments. Oxygen is a respiratory limiting factor at high temperatures and this effect is increased during acute warming scenarios, wherein there is no acclimation as organisms consume more oxygen when exposed to an abrupt temperature change than after an acclimation period (Bullock 1955; Kitching 1977).

Maximum feeding rate estimations are derived from functional response handling times (Juliano 2001). When the predator was non-acclimated the maximum feeding rate did not change with prey treatment but when the predator was acclimated the maximum feeding rate was far higher when prey were also acclimated. This indicates that when predator and prey populations undergo simultaneous acclimation to higher temperatures there will be a large increase in resource consumption, presumably due to the temperature mediation of the processes associated with handling time. When considered with the functional response types, it seems that simultaneous heating and acclimation produce an additive affect, which increases the maximum feeding rate and predator impact when prey is at 'high' densities. this must be caveated with the unreliable handling estimates of "Predator Acclimated", and "Both Unacclimated" which could be revealed under further investigation to have higher maximum feeding estimates.

There was a high variability in the shape of functional response in the different treatments with, justifiably, all three categorical functional responses observed. However, Type I functional responses require simultaneous handling and digestion and thus are only reported definitively amongst filter feeders (Lehman 1976; Jeschke, Kopp & Tollrian 2002, 2004). The intermediate response that was modeled is likely due to the low densities of prey supplied during the treatments (Jeshke, Kopp & Tollrian 2004), or the lack of habitat complexity in the experimental arena reducing handling limitations. As such, the results indicating Type I boundary responses may not directly reflect feeding ecology in the wild, but in this case serve as a comparison between the relative differences in parameter values. The results obtained were modeled as Type III responses due to the difference in proportional consumption. A Type III functional response was prevalent in trials at temperature apart from "Prey Acclimated". The change from Type II to Type III is concordant with other studies using fish predators which report shifts with environmental changes (Koski & Johnson 2002; Alexander *et al*. 2012), but contrasts with Wasserman *et al*. (2016b), which observed no functional response change in an invertebrate predator – prey system over various temperatures and habitat complexity. The Type III response when both were acclimated may be accounted for by the increased movement at high temperature (Biro *et al*. 2010) causing low consumption at low resource densities, but as the prey density increases there is a higher encounter rate and thus higher consumption. Furthermore, it is considered that when mortality is independent of foraging, foraging activity should increase concomitantly with resource availability (McNamara & Houston 1994). This would be the case when related to *S. canicula* in the Irish Sea where they are under low predation pressure. "Both Acclimated" had the highest magnitude functional response, while "Prey Acclimated" had the lowest. As "Prey Acclimated" functional response intensity was less than "Ambient" it suggests that the effect of temperature acclimation on *E. marinus* is more profound than on the predator, potentially because of the small body size of *E. marinus* giving the prey a metabolic advantage as the increased metabolic demands are mitigated by the small body size compared to the larger predator (Lincoln 1979; Whiteley 2011; Reuman *et al.* 2014; Di Santo & Lobel 2016).

The combined additive effects of predator and prey acclimation appear to increase predator impact, while temperature increase drives a shorter handling time

despite reducing the attack rate. While the present study deals specifically with juvenile lesser-spotted dogfish the results remain informative of the changes that temperature exerts on predation. This could have implications on the impacts of wild populations of *S. canicula* as they show spatial segregation by sex, temporal segregation and varying thermal strategies (Sims *et al*. 2001) as this may mediate the predation impacts when moving between thermally varied micro-climates. It is considered that when functional response is delivered as a phenomenological tool, the focus shifts from the shape of the response to the relative differences in parameter estimates (Lehman 1976; Jeschke *et al*. 2002; Alexander *et al*. 2012). This is due, in part, to the laboratory set up being inherently dissimilar to the conditions in sitú with regards to variation in temperature, prey availability, arena size, lack of refugia and habitat complexity. Nonetheless, we have provided a useful parameterization of the differences in resource consumption when predator and prey are factorially exposed to temperature increase.

This study demonstrates the importance of temperature as a regulating driver of predation. Temperature has the ability to increase predation pressure. Due to the high densities of dogfish (Richardson, 2016), increasing population size (Richardson 2016), and high discard survival rate (Revill *et al*. 2005), there is likelihood that predation on important fisheries species will increase. However, due to the generalist feeding strategy (Murdoch 1969) and patchy spatial distribution of prey, the Type III response is likely to prevail in the field (Trenkel *et al*. 2004). Furthermore, *E. marinus* may have an evolutionary advantage, due to body size, at higher temperatures (Genner *et al*. 2010; Di Santo & Lobel 2016), yet this may be mitigated when prey is found in high densities. The rate of warming, and subsequently environmental variation, affects maximum feeding estimates. Consequently, variation from the mean temperature is likely to have an impact upon predation pressure (Dell *et al.* 2011; Paaijmans *et al*. 2013; Vasseur *et al*. 2014). Furthermore, patchiness of prey populations could confer a benefit against predation, despite increased predation pressured conferred through decreased handling time. Though, it is necessary to caveat with the emphasis that thermal responses are species specific (Helmuth 2002; Broitman *et al*. 2009; Englund *et al*. 2011), as is the "environment" that each species experiences (Kearney 2006; Broitman *et al*. 2009), but also highly variable between individuals (Spicer & Gaston 1999; Calosi *et al*. 2013).

It is important to understand and quantify interaction strength in food webs and the how changes in abiotic context will affect predator-prey dynamics with regards to species and individual levels within a system (Calosi *et al*. 2013). The functional responses and associated parameters shown here demonstrate the differential responses within two organisms to a range of climatic scenarios. This will have implications for the sustainability of fisheries in the Irish and Celtic Seas, wherein there is high abundance of dogfish as acclimation to increased temperature increases maximum feeding rate but changes the proportional consumption of sparse prey populations.

Chapter 6

Relative impact assessment of species interactions under climate change and range shift scenarios

The following work from this thesis is currently in prep:

South, J., Dickey, J., Cuthbert, R., Dick, J.T.A. A new metric to assess relative impact potential under climate change scenarios

6.1 Introduction

Climate change is causing pervasive increases in mean values and variation in global temperature (Doney *et al.* 2009; Collins *et al*. 2013; Gunderson *et al.* 2017). These variations can drive a decline in biodiversity (Dawson *et al*. 2011), ecosystem function (Bascompte & Stouffer 2009) and community structure and dynamics (Harley *et al*. 2006; Doney *et al*. 2009; Garcia & Rosenberg 2010). Variation in thermal means can cause direct effects such as physiological change (Pörtner & Knust 2006; Calosi *et al.* 2013), and indirect effects such as interspecific interactions and trait mediated interactions (Huey *et al.* 2009; Schmitz & Trussell 2016) on community structure, size and dynamics (Norberg 2004; Angilletta 2009). Changing climate may alter the strength of interspecific interactions (Parmesan 2006; Gilman *et al*. 2010; Van der Putten *et al*. 2010; Laverty *et al.* 2017a). Interactions between species under projected climate change scenarios are currently vastly understudied (Gilman *et al*. 2010; Rosenblatt & Schmitz 2014; Gunderson *et al*. 2017) due to the difficult nature of modelling a suite of climate variables and experimentally manipulating conditions to deliver a robust and meaningful conclusion (Dawson *et al.* 2011). There is a considerable lack of empirical understanding of the way climate can mediate important interspecific interactions and thus they cannot be robustly incorporated into climate change predictions (Gilman *et al*. 2010).

It is well established that many species interactions are influenced by climatic change (Sanford 1999; Parmesan 2006; Van der Putten *et al*. 2010; Monaco & Helmuth 2011). Biotic interactions are known to structure ecological communities and can be drivers of declines in biodiversity (Bascompte *et al.* 2005; Angilletta 2009; Bascompte & Stouffer 2009) but can also increase biodiversity (Paine 1966). It is increasingly important to consider species as part of a web of interactions (Tylianakis *et al*. 2008; Van der Putten *et al.* 2010) as the differing vulnerability and responses of interacting predator-prey pairs to abiotic perturbations can be viewed as indicators of the vulnerability of whole assemblages (Monaco & Helmuth 2010; Dell *et al.* 2014). By breaking down assemblages into what Gilman *et al*. (2010) refer to as the "community module approach" it is possible to assess pairs of ecologically relevant, interacting predator-prey species to expound upon how climate change will impact on the interaction strength.

While it is acknowledged that prediction of climate change impacts over numerous levels is essential for future management and conservation (Kumschick *et al*. 2015; Urban *et al*. 2016), most models and frameworks proposed have focused on range shifts (Thomas *et al*. 2004; Graham *et al.* 2006; Ruegg *et al*. 2006) and the responses of one species towards one or more climatic variables (King *et al.* 2006; Bednaršek *et al.* 2012; Donelson *et al*. 2014; Gilbert *et al*. 2014; Bodmer *et al*. 2017). While these studies have disseminated important information as to the persistence of species and the structuring of systems, they generally do not consider the effect of biotic interactions, such as predator – prey interactions explicitly (Gunderson *et al*. 2016; Gunderson *et al.* 2017). This leaves a large gap in the knowledge of how climate may mediate the inherent dynamics that control population change (Van der Putten *et al*. 2010). A considerable amount of work has, however been focused on invasive species impact prediction (Dick *et al*. 2014; Alexander *et al*. 2015; Wasserman *et al*. 2016a,b; Laverty *et al*. 2017a,b; Dick *et al*. 2017a,b). This is due to the large cost of invasives to economies (Plank *et al.* 2016; Rouget *et al*. 2016) and biodiversity (Simberloff *et al.* 2013), and due to many invasions being facilitated by climate change (Walther *et al*. 2009; Mellin *et al*. 2016). It is both feasible and likely that climatic change may lead to species being facilitated into novel arenas through mechanisms such as range expansion (Grieve *et al.* 2016), ballast water (Ricciardi 2016), but it is also possible that native species may develop traits akin to invader effects (Valéry *et al*. 2008; Carey *et al.* 2012). This is due to ectotherms being directly affected by their environment, especially within marine systems, therefore changes in metabolism, predation and behaviour are all likely to occur (Brown *et al.* 2004; Dell *et al*. 2011; Dell *et al* 2014; Iacarella *et al.* 2015).

Community dynamics and interactions are a function of the environmental drivers they are exposed to, therefore, the prediction of the strength and direction of such relies upon gathering a mechanistic understanding of how these factors affect community levels (Denny & Helmuth 2009; Le Quesne & Pinnegar 2011; Laverty *et al.* 2017a,b). Therefore, to create an overarching prediction framework it is necessary to ensure that it takes into account consumer-resource interactions and contextual variables (Van der Putten *et al*. 2010; Gunderson *et al*. 2016; Gunderson *et al.* 2017). These are two drivers of ecological impact and it is important to consider them in concert if we are to develop early and effective management systems.

Many sources point to the necessity of developing a comprehensive, rapid, and reliable framework for predicting the population impact of climate change (Williams *et al.* 2008; Baum & Worm 2009; Van der Putten *et al.* 2010; Monaco *et al*. 2016; Stoffels *et al.* 2016). It is therein established that to do so, the framework must allow for: (1) a reliable prediction of climatic future (Araújo *et al*. 2005; Mills *et al.* 2013); (2) predator abundance (Baum & Worm 2009; Dick *et al.* 2017b); (3) resource availability (Baum & Worm 2009; Thomsen *et al.* 2011); (4) and empirical quantification of species interaction strength (Monaco *et al*. 2016; Dick *et al.* 2017a,b). Within such a framework, the prediction mechanism would ideally be standardised and universally applicable across systems to allow rapid identification and prediction of impact.

Current developments towards this end assess responses to climate change using Thermal Performance Curves (TPCs) (Huey & Slatkin 1976; Sinclair *et al*. 2016) where actual body temperature, environmental temperature and a trait such as locomotor speed, respiration or feeding rate is used as a proxy for fitness. Further, Monaco *et al.* (2016) developed the use of TPCs and combined them with Environmental Stress Models (ESMs) (Menge & Sutherland 1987; Menge & Olson 1990; Menge *et al.* 2002). ESMs determine whether a system under stress negatively affects the consumer more than the prey (Consumer Stress Model), or negatively affects the prey more than the consumer (Prey Stress Model). Thus, by combining TPCs using metabolic rate as a proxy, actual body temperature, ESMs and micro-habitat observations under a variety of temperature gradients, a new metric was developed to indicate the way increasing temperature may affect predator/prey performance. However, this stratagem has several shortcomings; the predominant issue is that the metric used was metabolic rate, therefore no feeding or predator behaviour was quantified. Predation rate has been shown to have differing thermal optima to metabolism or respiration rates (Pincebourde *et al*. 2008; Stoffels *et al*. 2016) and predatory behaviour and the handling behaviours associated with it are known to affect metabolic rate and oxygen consumption (Jobling 1981; Freitas *et al*. 2007; Fitzgerald-Dehoog *et al*. 2012). While Monaco *et al.* (2016) show differences in thermal preferences, they can only infer as to how these may affect the strength of species interactions. This leaves a degree of ambiguity as to how the thermal variation will affect population abundance, especially in light of numerous examples of ecological surprises and counter-intuitive responses in similar analyses (Crain *et*

al. 2008; Rosenblatt & Schmitz 2014). Furthermore, an integral piece of information is often omitted; resource abundance is rarely manipulated and assessed on its effect upon predatory behaviour under varying climatic conditions. Knowledge of limiting resources is necessary as high resource availability may potentially offset environmental stress (Thomsen *et al*. 2011; Gilman *et al*. 2017).

Functional response is a phenomenon that describes the consumption of a resource with regards to resource density (Solomon 1949; Holling 1959, 1965, 1966). Comparative functional response analysis has proven to be a reliable and powerful tool to predict and understand mechanisms behind invasive species impacts (Dick *et al*. 2014; Alexander *et al*. 2015; Dick *et al*. 2017a,b; Laverty *et al*. 2017a,b). Simple laboratory experiments can be used to assess consumer-resource interaction strengths across a variety of contexts (Barrios-O'Neill *et al.* 2014; Alexander *et al*. 2015; Wasserman *et al*. 2016a,b; Laverty *et al*. 2017a,b), for numerous species (Barrios-O'Neill *et al*. 2016; Laverty *et al*. 2017a,b) giving it huge comparative and predictive power. Additionally, functional response can be determined in sitú which is ideal for species that cannot feasibly be maintained in the laboratory (Smout *et al*. 2010; Smout & Lindstrøm 2007).

This approach takes into account the effect of both high and low resource availability on a consumers behaviour and allows insight into population and community dynamics of both consumer and resource. By determining and comparing the functional response of an invasive consumer against that of a native consumer under different contextual scenarios it is possible to assess the ecological impact through comparing magnitude functional response curve, and the associated parameters (attack rate, handling time, and maximum feeding rate) (Dick *et al.* 2014, Dick *et al.* 2017a,b). Maximum feeding rate estimations provide an empirical quantification of species interaction strength. The merit in the FR approach is that it is simplistic yet reliable, and that it provides rapid impact assessment making it straightforward for utilisation by stakeholders and policy makers (Hobbs *et al.* 2009; Hobbs *et al*. 2011; Dick *et al.* 2014; Dick *et al*. 2017a,b). Further, it allows prediction of impact for species with no prior invasion history, the means of which have not been available until now (Dick *et al.* 2017a,b).This means that the Functional Response methodology can be applied to native species and predicted invasives under projected climate change scenarios.

Dick *et al*. (2017b) and Laverty *et al.* (2017b) developed a new framework within which to rapidly and robustly predict ecological impact. The Functional Response (FR), i.e. the consumer *per capita* response (Holling 1959), is combined with the Numerical Response (NR), i.e. the consumer population response (Solomon *et al*. 1949, Holling 1959), or uses predator abundance (AB) as a proxy for NR, to determine a Total Response (TR) (Equation 6.1).

TR=ABxFR **Equation 6.1**

This is similar to the "Lonsdale-Parker equation", whereby invader impact is a function of range (R), abundance (A) and per capita effect (E) (I=RxAxE; Parker et al. 1999).
Merging these two metrics, Dick *et al*. (2017b) thus proposed an Impact Potential (IP) (Equation 6.2) that quantifies an absolute value for the IP of a species.

IP = AB x FR **Equation 6.2**

Equation 6.2 can then be adapted to describe the Relative Impact Potential (RIP) (Equation 6.3) of one species relative to another, in this case a native analogue (Dick *et al.* 2017b).

$$RIP = \left(\frac{\text{FR invader}}{\text{FR native}}\right) \text{x} \left(\frac{\text{AB invader}}{\text{AB native}}\right)$$ **Equation 6.3**

Equation 6.3 provides a quantification of interaction strength and ecological impact of one species on another, relative to another consumer. In cases where the RIP is <1 the invader will have less impact on prey populations than the native predator, when RIP = 1 the invader will have no impact above the native predator, and where RIP >1 there will be likely invader impact on prey populations. This allows the prediction of whether a species is going to be ecologically damaging under specific circumstances.

To incorporate uncertainty into the RIP the probability density function can be determined using the SD and means of the FR and AB. Equation 6.4 thus includes the pdf (*f*) into the RIP metric.

$$f(\text{RIP}) = \left(\frac{f(\text{FR invader})}{f(\text{FR native})}\right) \text{x} \left(\frac{f(\text{AB invader})}{f(\text{AB native})}\right) \qquad \textbf{Equation 6.4}$$

This method has been shown to be effective in predicting measurable changes in populations of ecologically relevant prey species (Laverty *et al*. 2017b). Though data may be deficient in some cases, field abundance can be estimated. The method therein, shows a simple and powerful way of deriving ecologically relevant impact prediction (Dick *et al.* 2017a,b; Laverty *et al.* 2017b). The combination of RIP calculations (Dick *et al.* 2017b) and the biplot schematic in Laverty *et al*. (2017b) can show clear impact potential of predator-prey systems under climatic stress scenarios.

I postulate altering the method described to give ecologically relevant predictions of native and invasive species under climate change scenarios as these have many similarities to situations where there is no invasion history. This methodology combines *per capita* response with resource availability and predator abundance under the context of climatic scenarios in a rapid and clear mechanistic assessment of the relative potential impact of a predator (Hijmans & Graham 2006; Baum & Worm 2009).

6.2 Methods

In order to assess the ecological impact of a species under climate change scenarios Equation 6.3 and Equation 6.4 (Eqn 4 and Eqn 5 in Dick *et al.* 2017b) can be modified to become Equation 6.5 and Equation 6.6, wherein instead of invader and native it is now a relative comparison for a single species under higher temperature and lower temperature conditions. This uses the FR and AB estimates for one species under different thermal scenarios to produce an RIP score in the same way as Equation 6.3 and Equation 6.4.

$$\text{RIP} = \left(\frac{\text{FR Higher Temp.}}{\text{FR Lower Temp.}}\right) \text{x} \left(\frac{\text{AB Higher Temp.}}{\text{AB Lower Temp.}}\right) \qquad \textbf{Equation 6.5}$$

$$f(\text{RIP}) = \left(\frac{f(\text{FR Higher Temp.})}{f(\text{FR Lower Temp.})}\right) \text{x} \left(\frac{f(\text{AB Higher Temp.})}{f(\text{AB Lower Temp.})}\right) \qquad \textbf{Equation 6.6}$$

Equation 6.6 uses the SD and means to find the uncertainty around the RIP score using the pdf. This is a laborious and complex process that requires information that is often difficult to obtain. Therefore, by correlating the data in Table S1 in Dick *et al.* (2017b) I demonstrate that the results from Equation 6.3 and Equation 6.4 are closely correlated ($p < 0.001$; Fig. 6.1 & $p<0.001$; Fig. 6.2). This justifies the use of the simpler Equation 6.3 and therefore Equation 6.5.

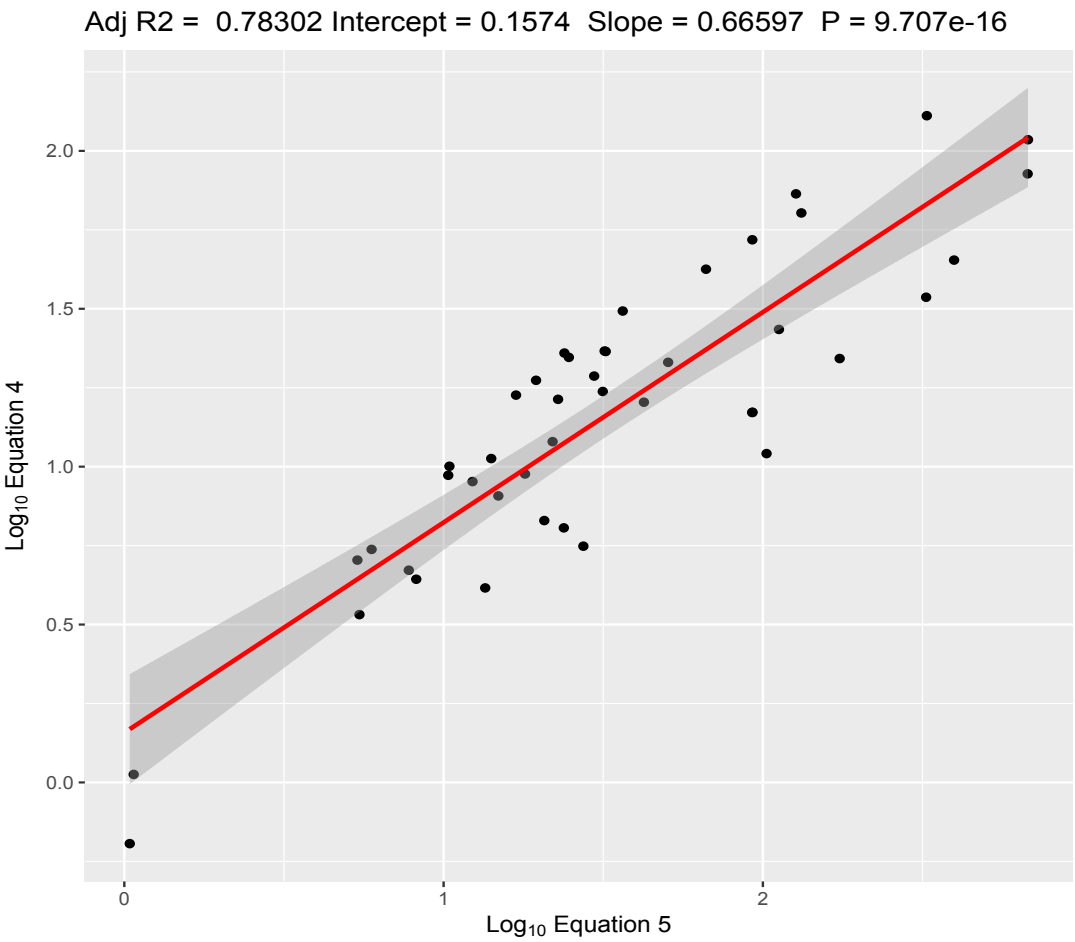


Fig. 6.1 Log_{10} regression of Method 1 of Equation 4 and Equation 5 data from Table S1 in Dick *et al.* (2017b)

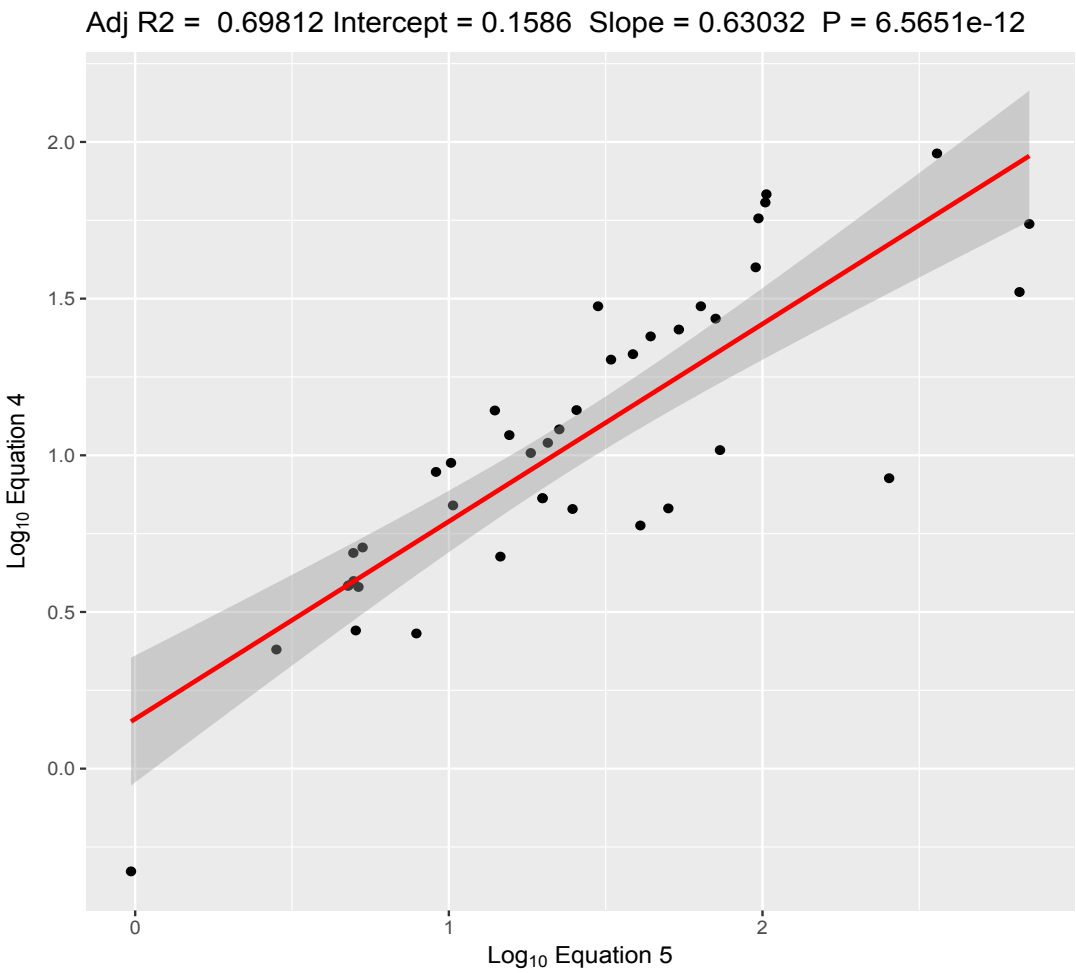


Fig. 6.2 Log_{10} regression of Method 2 of Equation 4 and Equation 5 data from Table S1 in Dick *et al.* (2017b)

6.2.1 Resource Reproductive Qualifier

Prey abundance has the potential to change with temperature, therefore it is an important addition to assess whether there will be an increase or decrease in prey population with the temperatures investigated. As such, this change in prey abundance has the potential to either depress or enhance the RIP value, as an increase in prey abundance would offset an increase in predator impact while a decrease in prey abundance could increase predatory impact. Therefore, a "Resource Reproduction Qualifier" (RRQ) is incorporated into Equation 6.5. This takes the form of the reciprocal of the factor by which reproduction is affected by temperature change, this becomes Equation 6.7.

$$RIP_q = \left(\frac{\text{FR Higher Temp.}}{\text{FR Lower Temp.}}\right) x \left(\frac{\text{AB Higher Temp.}}{\text{AB Lower Temp.}}\right) x \text{RRQ} \qquad \textbf{Equation 6.7}$$

6.2.2 Dogfish

Data on juvenile dogfish (34.82±2.77 SD cm total length) functional response type and maximum feeding rate estimate were taken from South & Dick (2017) (Chapter 5), wherein two temperature treatments were used to simulate current temperature (11.3°C) and predicted summer mean temperature (16.3°C) (Sokolov *et al*. 2009; See Chapter 5 for further detail). Prey used in this study was the amphipod *Echinogammarus marinus*. We used the data from the "Ambient" treatment and "Raised" treatment for our analysis. At 11.3°C "Ambient" there was a maximum feeding rate (hr^{-1}) of 12.37±1.67 SE and a Type II functional response and at 16.3°C "Raised" treatment there was a maximum feeding rate (hr^{-1}) of 29.42±4.23 SE (Chapter 5; South & Dick 2017). There were significant differences between the maximum feeding rate estimates ($t=3.74$, $df=30.91$, $p<0.001$) (Chapter 5; South & Dick 2017).

Data on dogfish abundance were collected over 02/03/15-22/03/15 as part of the AFBI March groundfish survey on the RV Corystes in the Irish Sea (see Chapter 4 for details). (See Appendix 1 for specific haul details and locations). Dogfish abundance was 25.60±41.82 SD M^2 (nautical mile), this abundance estimate was used for the baseline 11.3°C treatment.

Data on gestation time and fecundity were used to estimate a potential population change under a raised temperature regime. In UK waters gestation time is around 273 days but in waters 10°C and under eggs can be retained for up to a week longer (Ballard *et al.* 1993). In warmer waters (16°C) gestation time is 145-175 (194±24 SD) days (Ballard *et al*. 1993). This is a decrease of 35.89-46.88% in gestation time. Dogfish fecundity is estimated 26-62 eggs a year in the North East Atlantic (Ellis & Shackley 1997) and estimates of 96-115 and 45-190 eggs per female a year in the Tunisia and the Gulf of Lion (Capapé 1977; Capapé *et al.* 1991) where temperatures are higher. This is a percentage increase with a lower limit of 35.41% and upper limit of 86.31%. It was assumed that fishing pressure stayed the same. With this information in mind it was estimated that there could feasibly be a dogfish population increase of 30-50% with increased temperature.

Prey abundance data was collated from Maranhão & Marques (2003) wherein fecundity and rate of embryonic development of *Echinogammarus marinus* were found to have no significant difference at 10°C and 15°C. Therefore, in this case it could be safely assumed that for the temperatures investigated that there is no change in prey population. However, it is noted in that at higher temperatures there is a decrease in body size, faster maturation and a shorter lifespan in *Echinogammarus marinus* at increased temperature (Maranhão *et al*. 2001; Maranhão & Marques 2003). This trend holds true in other amphipod species such as *Gammarus locusta* (Neuparth *et al*. 2002). Thus, the prey population probably will not experience any temperature driven population size changes at the temperatures investigated in the dogfish experiment, making RRQ = 1.

6.2.3 Shanny

Data on shanny functional response and maximum feeding rate was taken from Chapter 3, using the non-replacement method data. There were three temperature treatments investigated of 15°C, 17°C and 19°C. Prey used in this study was the amphipod *Echinogammarus marinus*. A Type II functional response was found at 15°C and17°C, there was a shift to a Type III functional response at 19°C. 15°C had a maximum feeding rate (hr^{-1}) of 17.28±2.21 SE, 17°C had a maximum feeding rate (hr^{-1}) of 19.64±3.15 SE, and 19°C had a maximum feeding rate (hr^{-1}) of 7.61±2.12 SE.

Data on shanny abundance was collected via a survey at Walter's Shore. Transects (n=5) of 10m were carried out vertically down the shore line at low tide, a search area of 1m each side of the transect line was maintained to allow a total search area of 100m^2. Searching involved lifting cobbles and large rocks and searching under seaweed to count the total number of fish found. All searching was carried out by the same surveyor to avoid observation bias. Overall there were 0.33±0.30 SD m^2, this population estimate is aligned to the 15°C temperature treatment due to representing the current population and current summer high temperature (See Chapter 3).

Shannys have a wide distribution in the Northern Hemisphere and are found to spawn in the cooler months of the year (Almada *et al*. 1990), therefore at their Southern limit in Portugal breeding takes place in December-February at a temperature of 14°C-17°C (Almada *et al.* 1990), whereas the population in Great Britain and Ireland breeds from April-August (Zander 1986). Taking this into account, it can be assumed that at our treatment temperatures of 15°C and 17°C that the population stays the same. However, due to warming temperatures to 19°C the breeding season in the British Isles may potentially be shortened from a five month period to a two month period, resulting in a 60% loss of breeding season. Therefore, it could be inferred that there may be a potential 60% population decrease due to lack of suitable breeding temperature.

At 20°C there is a significantly shorter embryonic development (48%), and significantly less fecundity (27%) in *Echinogammarus marinus* (Maranhão & Marques 2003). It could thus be considered that there may somewhat be a small decrease in prey population size with warming temperatures. Therefore, we have included in our calculations the consideration that the prey population may be subject to a 15% decrease (at the 19°C shanny treatment) in population to demonstrate how the potential impact of shanny on prey populations may be affected. This makes the RRQ = 1 at 15°C and 17°C (See 6.2.2), and RRQ=0.85 at 19°C.

6.2.4 Lionfish

Lionfish data on functional response and maximum feeding rate was taking from Chapter 2, using the data from 22°C (low temperature) and 26°C (high temperature). Prey used in this study was *P. varians*. Type II responses were found at both treatments. 22°C had a maximum feeding rate (hr^{-1}) of 4.34±0.55 SE, and 26°C had a maximum feeding rate (hr^{-1}) of 8.34±0.65 SE.

Lionfish have an invasive range and a native range, in their native range they are subject to temperatures of 28°C-30°C (temperature estimates from Guam and Phillipines in Cure *et al*. 2012) and a possible temperature range of 16°C-30°C in the Atlantic invaded range (Whitfield *et al*. 2006; Cure *et al.* 2012; Grieve *et al.* 2016). Therefore, abundance data was collated for the Pacific Ocean (1.70±2.27 SD ha^{-1}) and Indian Ocean (28.80±1.75 SD ha^{-1}) (Kulbicki *et al.* 2012) to represent the native abundance at the higher temperature for comparison in the biplots. Abundance for the invaded range was 21.20 ±5.1 SD ha^{-1} at low temperature (20°C at Cape Hatteras; Whitfield *et al*. 2006) and 393.00±144.4 SD ha^{-1} (Green & Côté 2009) at high temperature (The Bahamas, temperature estimates from Cure *et al*. 2012). While experimental temperature treatment is somewhat lower in the high temperature treatment than that experienced in the wild (27-31°C), the temperature reported is from June-September warm periods (Cure *et al*. 2012) and this is being assessed with relevance to further potential invasion sites liable to cooler temperatures.

Data on *P. varians* reproduction and fecundity was variable but there is faster development time and fewer instars at higher temperature (17°C-30°C around 10% faster) but fecundity does not change (Oliphant *et al*. 2014). Kim (2010) found the survival of another carridean shrimp, *Palaemon serrifer* to be 15% more successful when temperature was increased from 15°C-25°C. Overall, it could be suggested that there may be a 5% increase in prey population when temperature is increased across the high and low temperature treatments investigated, making the RRQ = 1.05.

6.3 Results

6.3.1 Dogfish

There is a clear shift towards a higher impact potential when temperature is increased due to the increased dogfish population under the temperatures investigated (Fig. 6.3). The RIP score is >1 for both 30% and 50% population increase at the raised temperature (Fig 6.4). Due to the RRQ being 1 there is no change to these scores when the prey population is considered, making RIP_q the same as RIP (Fig 6.4).

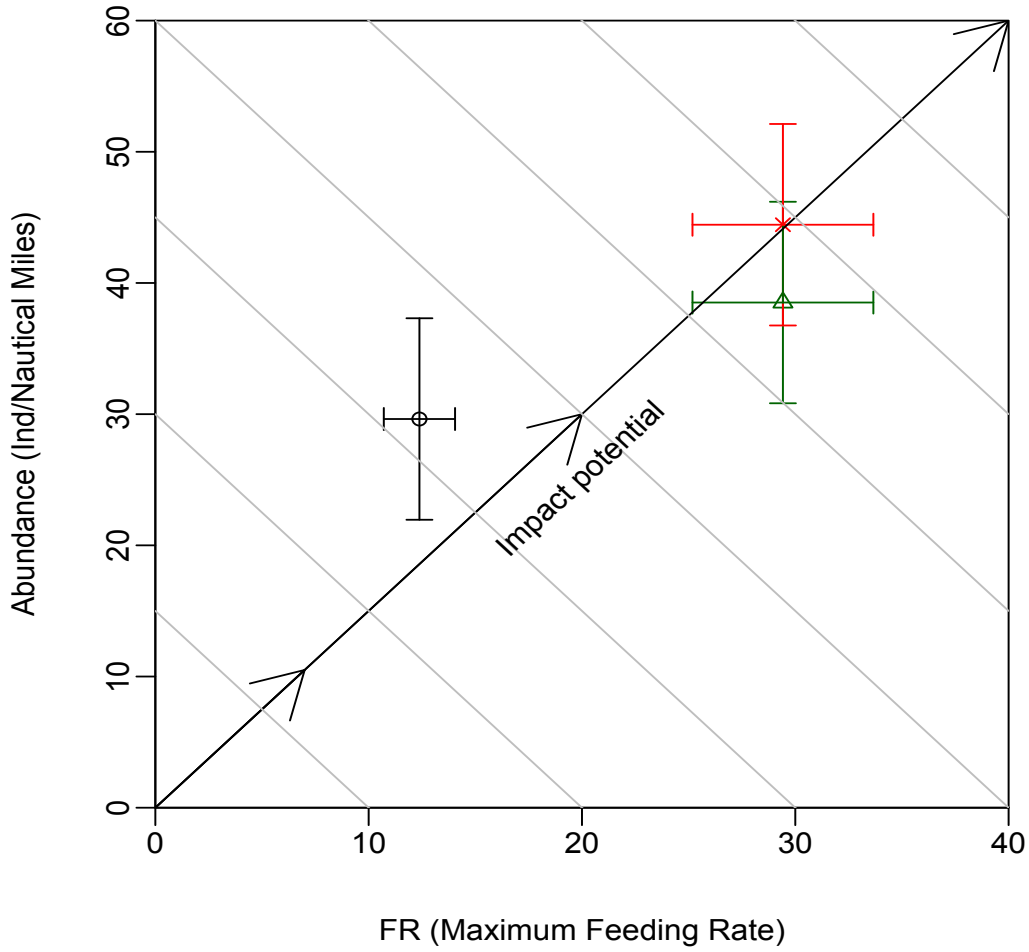


Fig. 6.3 RIP biplot showing the mean±SE for dogfish in the Irish sea at 11.3°C and 2015 population (○), 16.3°C at a 30% population increase (△), and 16.3°C at a 50% population increase (×)

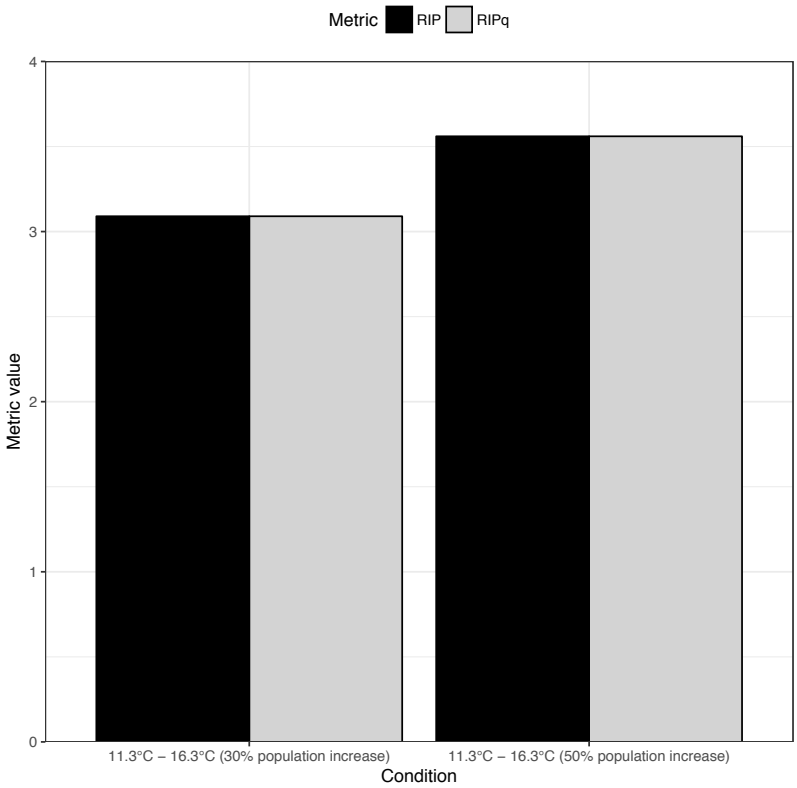


Fig. 6.4 Bars showing changes in RIP (black) and RIP_q (grey) value when RRQ is applied for dogfish at 11.3°C - 16.3°C at a 30% population increase, and 11.3°C - 16.3°C at a 50% population increase

6.3.2 Shanny

There is a similar degree of impact at 15°C and 17°C, with 17°C being marginally higher (Fig. 6.5). There is a shift in impact with increased temperature to 19°C whereupon the ecological impact of the shanny is decreased due to both maximum feeding rate and abundance decreasing (Fig. 6.5). The RIP score was >1 when temperature is increased from 15°C to 17°C, at the other temperatures the RIP score was <1 (Fig 6.6). The RRQ score increases the RIP_q when temperatures are raised to 19°C, however the RIP_q scores for 15°C-19°C and 17°C-19°C still remain <1 (Fig 6.6).

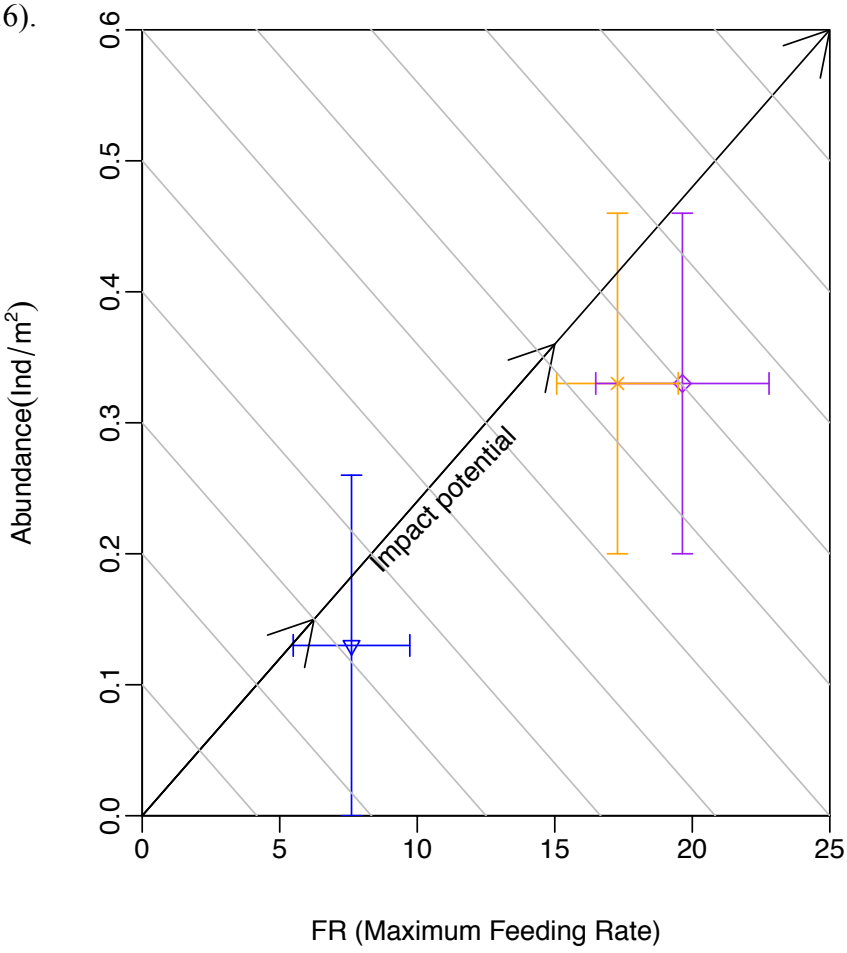


Fig 6.5 RIP biplot showing the mean±SE for shannys at 15°C (×), 17°C with a 30% population increase (◇), and 19°C with a 60% population decrease (▽)

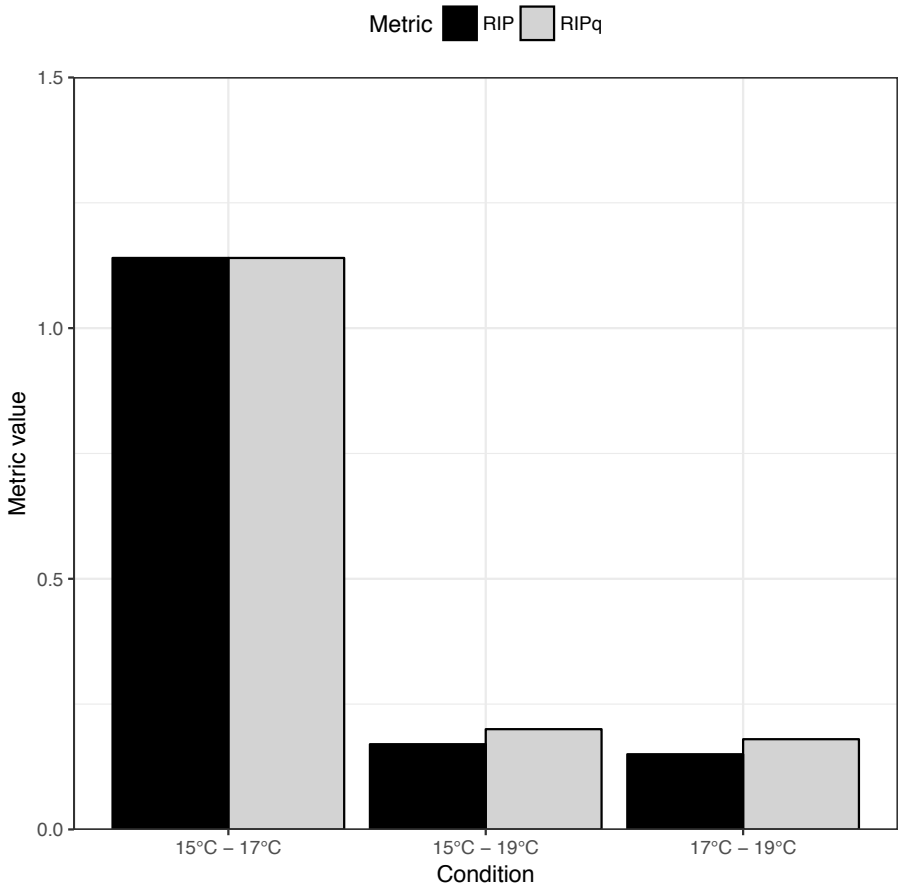


Fig. 6.6 Bars showing changes in RIP (black) and RIP_q (grey) value when RRQ is applied for shannys at 15°C - 17°C, 15°C - 19°C and 17°C-19°C

6.3.3 Lionfish

The high temperature Atlantic invaded range shows a large increase in impact potential compared to the low temperature invaded range and the two high temperature native range values (Fig. 6.7). The impact increase is mainly driven by the increased abundance at the high temperature invaded range (Fig. 6.7). The lionfish abundance in their native range is similar to the abundance at the low temperature invaded range which dampens the relative impact (Fig. 6.7). The RIP score was >10 and due to the RRQ of 1.05 there is a slight decrease to make the RIP_q = 33.93 (Fig 6.8).

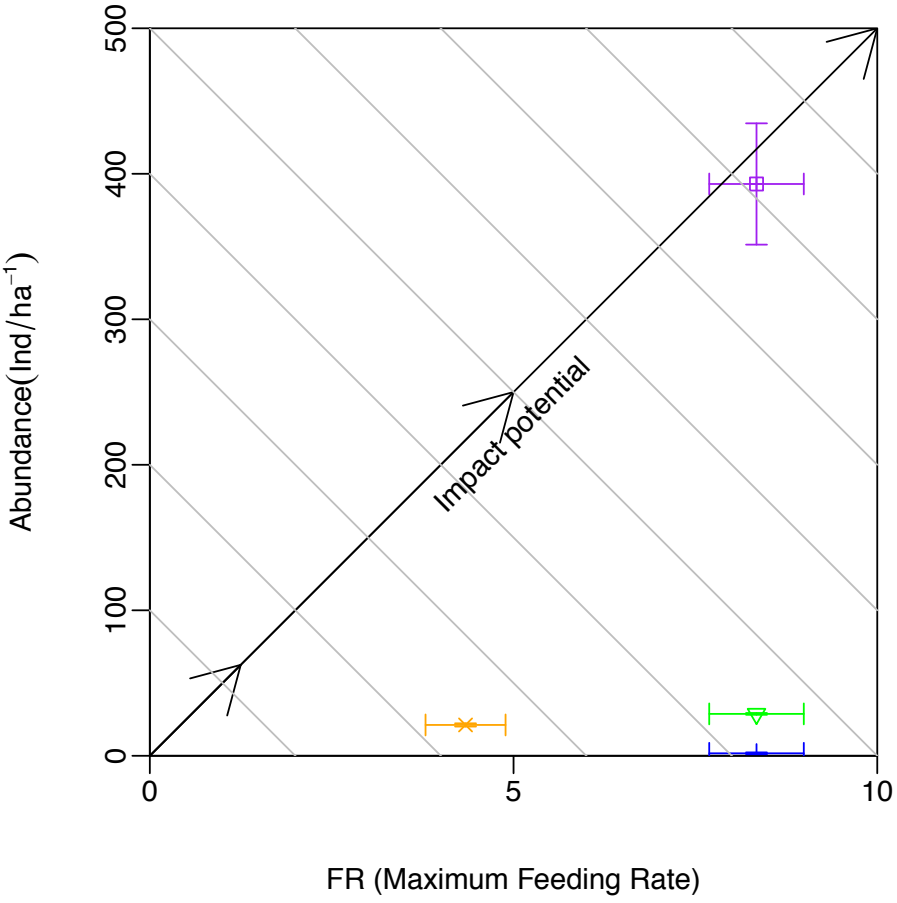


Fig. 6.7 RIP biplot showing the mean±SE for lionfish at low temperature in the Atlantic invaded range (22°C) (×), high temperature in the Atlantic invaded range (26°C) (□), high temperature in the Pacific native range (26°C) (+), and high temperature in the Indian Ocean native range (26°C) (▽)

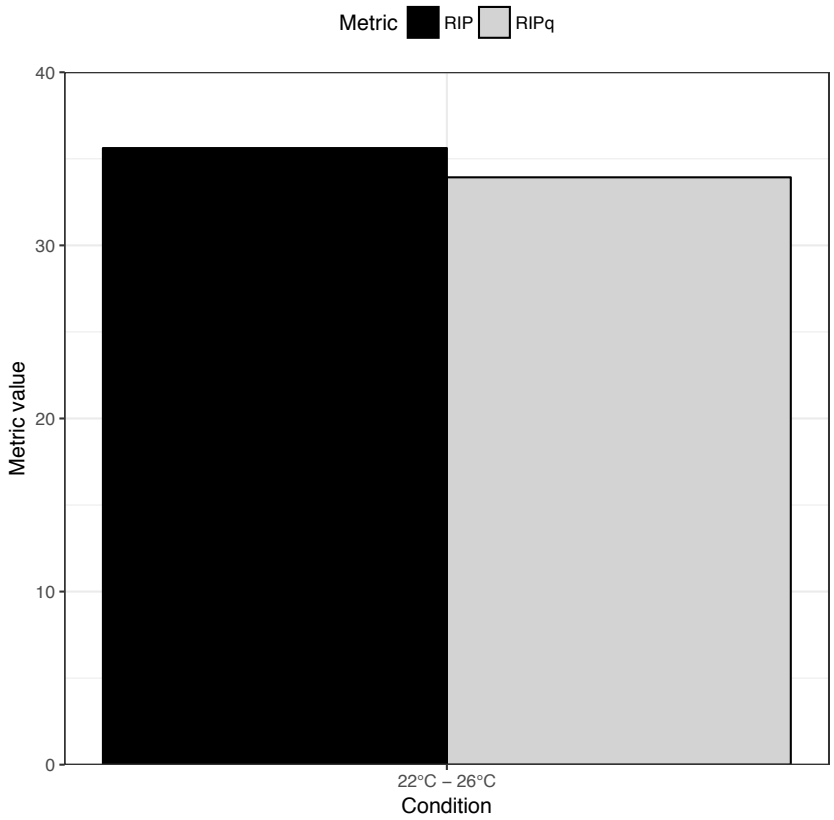


Fig. 6.8 Bars showing changes in RIP (black) and RIP_q (grey) value when RRQ is applied for lionfish at 22°C - 26°C

6.4 Discussion

Using the metric conceived by Dick *et al*. (2017b) and Laverty *et al*. (2017b) I provide a comprehensive illustration of the changes expected in the predatory impact of a number of species under expected future temperatures (dogfish and shanny), and under potential temperatures experienced due to further invasion (lionfish; (Turan *et al.* 2014; Oray *et al.* 2015; Kletou *et al.* 2016; Azzuro *et al*. 2017). By adapting this metric to refer to climatic change rather than an invasive comparison we provide a way to rapidly quantify ecological impact on prey populations. The addition of the RRQ takes into account expected thermally driven changes to prey populations and incorporates these to represent their effect (or lack of effect) upon the RIP score. In this way I demonstrate a prediction metric that accounts for (1) predator abundance (Baum & Worm 2009; Dick *et al.* 2017b); (2) resource availability (Baum & Worm 2009; Thomsen *et al.* 2011); (3) and empirical quantification of species interaction strength (Monaco *et al*. 2016; Dick *et al.* 2017a,b).

6.4.1 Dogfish

The temperatures used reflects the potential daily 3-5°C global (SST) increase (Sokolov *et al.* 2009). The RIP biplot schematics show a clear increase in impact, driven by both the increase in maximum feeding rate and the suspected increase in population. It should be further considered that the effect of temperature on maximum feeding rate could be more pervasive than the population change i.e. the numerical response, as if there was no change in predator population, in this case there would still be a considerable increase in impact potential. The RIP calculations show a numerical visualisation of change that reflect the RIP biplot change. The temperatures investigated did not elicit a change in prey population through mediation of development times or fecundity, therefore demonstrating that sometimes the RRQ will be held at 1. Temperature has a clear effect on the *per capita* impact of dogfish (Chapter 5; South & Dick 2017). When combined with the potential population abundance increase it is clear that increasing temperature causes a substantial increase in the potential predatory impact of dogfish on prey populations.

Feeding rates are driven by body size in addition to contextual factors (Gillooly *et al*. 2002; Rall *et al*. 2012; Barrios-O'Neill *et al*. 2016). In this study (Chapter 5) the dogfish were juveniles therefore reducing the body mass ratio, it could be considered that the true maximum feeding rate of adult dogfish on this prey would be higher due to allometric scaling (Vucic-Pestic *et al*. 2010; Rall *et al*. 2012). Elasmobranchs are usually classed as "K-strategists", referring to the long gestation times, low fecundity, large body size, and delayed maturation times (King & McFarlane 2003). Usually K-selected species are at risk to over exploitation by predation, fishing, and abiotic perturbations due to their life history traits (Galluchi *et al*. 2006) but dogfish pose an anomaly to this generalisation. Populations of lesser spotted dogfish are stable and increasing in the Irish Sea (Richardson 2016) and have a higher fecundity than other teleosts (Capapé 1977; Fischer *et al.* 1987; Spencer & Collie 1995). This is because they are not a targeted fishery in the Irish Sea (Richardson 2016) and have a >90% survival rate when discarded (Kaiser & Spencer 1995; Revill *et al.* 2005; Rodriguez-Cabello *et al*. 2005). Therefore, with slow warming scenarios and lack of predation pressure and exploitation they have increased hugely in abundance (Sguotti *et al*. 2016; Richardson 2016). This means that they are potentially exerting a huge amount of top down pressure on the Irish Sea system, which is set to only increase in the future, especially if fishing pressure and practices remain the same. These results suggest that in the future there could be a predatory impact generated equal of that of the Chinese mitten crab (*Eriocheir sinensis*) (Dick *et al*. 2017b). This supports the hypothesis that in the future climate change could cause native species to develop traits associated with invasive species (Valéry *et al*. 2008; Carey *et al.* 2012).

6.4.2 Shanny

Temperature increase to 19°C elicited a considerable reduction of predatory impact in comparison to the biplot results for 15°C and 17°C. This seems to be driven by additive factors of decreased maximum feeding rate and decreased predator abundance at 19·C. Consequently, this result is somewhat increased by the RRQ being 0.85 due to a decrease in prey fecundity at this temperature despite the faster development times (Maranhão & Marques 2003) but this increase has a negligible effect. Due to the decrease in predator population at 19°C, only the

increase from 15°C-17°C has an RIP of >1, despite the higher maximum feeding rate at 17°C.

This indicates that shorter term warming will have a discernible impact upon prey population abundances, but it still remains small in comparison to the other results obtained in this study. The RIP and RIP_q values under these temperature treatments provide a differential story to that of the dogfish, which indicates how important it is to consider predator and prey dynamics and life history changes under thermal regimes. Further, it indicates that there could be a shift in predation pressure under increased temperature, which in this case may reduce pressure on prey populations.

The results suggest that the shanny, as an intertidal fish, is subject to a mechanism which reduces their ecological impact under high temperatures. Perhaps due to the high degree of thermal variability in the intertidal zone providing them with "warm pre-conditioning" and therefore some degree of protection (Hawkins & Warner 2017; Marigómez *et al.* 2017). This is in contrast to the metabolic theory of ecology (Brown *et al.* 2004; Englund *et al*. 2011) indicating that there should be further investigation into the mechanics of thermal responses. This is important especially considering intertidal species that are physiologically predisposed to being resilient against environmental variation, as there is growing evidence that organisms exposed to preconditioning or chronic thermal stress develop protective physiological traits (Hawkins & Warner 2017; Marigómez *et al*. 2017).

6.4.3 Lionfish

The biplot metric indicates how lionfish ecological impact is vastly constrained by the lower temperature treatment through the mediation of both feeding rate and lower abundance. Further, when comparing the abundances with their native ranges in the Pacific and Indian Oceans (Kulbicki *et al*. 2012), the importance of including the NR in the metric is emphasised due to their comparatively similar temperatures within the Atlantic invaded range (Kulbicki *et al.* 2012) and therefore equivalent maximum feeding rates, but highly disparate population abundances compared to the higher temperature invaded range. It should be confirmed here that the densities used for the Atlantic invaded range are described as "record densities" (Green & Côté 2009) and therefore are on the extreme side.

Additionally, this survey was undertaken in 2009 on a small patch in New Providence, Bahamas (Green & Côté 2009) and as such is not wholly representative (See Hackerott *et al.* 2017 for notes on lower lionfish densities). In defense of using this estimation, it provides an upper estimate limit and shows the possible extremes of lionfish colonisation and settlement in the Atlantic invaded range. However, using the method supplied it is relatively simple to calculate context dependent (i.e. location) calculations for RIP and RIP_q, which may prove helpful for the ongoing management of these damaging invaders.

The RIP_q value for lionfish at this temperature increase puts them at an impact factor similar to *Pseudorasbora parva* (Topmouth gudgeon) (Dick *et al*. 2017b), but this only takes into account the impact change from 22°C-26°C. If compared between native and invaded range only, the impact is likely to be lower due to the effect of temperature on feeding rate being removed from the consideration. This again, highlights the effect of the NR on RIP and emphasizes the importance of the incorporation of NR into prediction metrics (Dick *et al.* 2017a,b; Hackerott *et al*. 2017; Laverty *et al*. 2017b).

6.4.4 Conclusion

The RIP metric has been successfully used to predict the potential impact of a variety of predators under the context of climatic change or temperature change due to invasion. This study highlights the utility of the RIP method in a novel prediction exercise. By comparing predicted scenarios with current ones, it is possible to quantify relative change and give a mechanistic explanation as to what is driving ecological impact (Dick *et al*. 2017b; Laverty *et al*. 2017b). While the data in this Chapter deals specifically with the same species under two different abiotic contents, the merit of this method is that it could also be used to predict and quantify the relative impact potential of an invasive species compared to a native species under future climatic scenarios. Policy makers can use this as a tool to understand how native and invasive species may become ecologically and economically damaging in the future and use the information to implement mitigation and intervention measures to reduce damage.

The value of the addition of the RRQ to the RIP is demonstrated here as it acts to enhance or dampen the RIP depending on the effects. Thermal regime can

affect metabolism (Arrhenius 1889; Brown *et al.* 2004), fecundity (Frommel *et al*. 2010; Miller *et al*. 2015), and development time (Garrido *et al.* 2016) of a variety of species, in this case the temperatures investigated caused a myriad of effects on both predator and prey population dynamics and life histories. The differential effect of this is shown here wherein the RRQ >1 in the lionfish example, but <1 in the shanny example. This methodology delivers a succinct way of quantifying impact potential while considering many variables.

Our results substantiate the assertion by Dick *et al.* (2017b) that low impact or native species would have RIP and RIP_q scores <1. Context is an important determinant of the way species interactions (Alexander *et al*. 2015; Barrios-O'Neill *et al*. 2014; Laverty *et al*. 2017a), but also of abundance between different contexts (Laverty *et al*. 2017b). Therefore, this method lends itself as a framework for localised impact predictions, allowing contextually informed mitigation plans to be created.

The way in which maximum feeding rate is obtained can be described as simplistic, as it lacks further context that may mediate the functional response, nonetheless, these can be further incorporated into factorial experiments (Barrios-O'Neill *et al*. 2014; Laverty *et al*. 2017a,b). Abundance and predator/prey population relationships with temperature can be difficult to obtain and therefore qualified assumptions have to be made in some cases. This gap in empiracal data could be bridged by using heuristic population dynamics data as a proxy to allow an informed conclusion to be made. Despite this, the evidence provided gives a reliable proxy for consumption rates across the board, and when combined with information on the numerical response of predators and the RRQ, it is capable of delivering a rapid relative impact assessment of predators under different climatic contexts (Dick *et al*. 2017b; Laverty *et al*. 2017b).

Chapter 7

Synthesis

7.1 Overview

Species interactions and their associated strengths (*per capita* effect) are the driving force behind ecosystem dynamics and species population abundances (Berlow *et al*. 2004; Brose *et al*. 2008). Therefore, they remain a priority to quantify in order to understand and manage valuable resources in a sustainable manner. Changing abiotic parameters have differential effects on a species level, depending which species is experiencing the change (Chapter 2, 3, 5, 6) (Englund *et al*. 2011; Lang *et al*. 2012; Sentis *et al*. 2015). This thesis details examples of the way in which abiotic change can mediate the ecological impact of a consumer and the issues these may pose to the sustainability of Northern Irish sea fisheries.

Climatic change and increasingly connected systems are well known to facilitate movement of species (Perry *et al*. 2005). Using a case study of one of the most damaging and well reported marine invasions (lionfish), I assessed ways in which the ecological impact may change under variations in temperature, habitat complexity and light wavelength. Thus, giving an empirical quantification of predation under different variables in a standardised manner. This supplies valuable information as lionfish continue to colonise new territory (Andradi-Brown *et al*. 2017). My results demonstrate a high *per capita* (FR) and high numerical response (Chapters 2 & 6) which gives a higher potential impact at the higher temperature treatment.

Using field survey methods to understand predator distribution, diet, and prey selectivity (Chapter 4) supplies valuable information on the current population of predators and the way in which they exploit resources. Results from Chapter 4 on the diet and abundance of dogfish in the Irish Sea pinpointed them as a species of interest and potential threat to fisheries sustainability in the future. This was then used to give further depth to the information determined from FR analyses (Chapter 5).

By adopting thermal change as a ‘master variable’, I detail in Chapters 2, 3, 5 and 6, the ways in which the predatory impact of an invasive species (lionfish) and native species (dogfish and shanny) is affected under different levels of thermal change and differential thermal acclimation regimes. In Chapter 4 I highlight the importance of dogfish as an abundant elasmobranch predator in the Irish Sea. Further, in Chapter 5 by taking into account the acclimation of a prey species I show

a novel result in which identical acclimation treatments of predator and prey have an additive interaction effect on the maximum feeding rate of dogfish. Whereas other treatments resulted in similar maximum feeding rates that were significantly lower than when both species were acclimated. Finally, in Chapter 6, I provide a possible metric, altered from a proven invasive species impact prediction metric, which can be used in management systems as an impact potential predictor of species impact under future climatic change. This delivers a cohesive and empirical assessment of impact while considering *per capita* response, numerical response (abundance), prey life history and population dynamics.

7.2 Invasion specific findings

The movement of lionfish in the Atlantic was likely initially started through accidental release (Randall 1987), however, more recently there has been signs of settlement and a sustained invasion in the Mediterranean (Turan *et al.* 2014; Oray *et al.* 2015; Kletou *et al.* 2016; Azzuro *et al.* 2017; Turan *et al*. 2017). This is suggested to be part of an Erythrian invasion via the Suez Canal (Barriche *et al*. 2017). Models have suggested that colonisation of waters around the United Kingdom are unlikely due to current patterns and critical thermal limits (Johnston & Purkis 2014). However, Turan *et al.* (2017) demonstrate lionfish active feeding and overwintering at 14-16°C in Turkish waters. Nonetheless, the lionfish remains a concerning invader and an extreme worst-case scenario style case study of a marine teleost invader.

My results in Chapter 2 suggest that lionfish have a persistent Type II functional response, making them a potential destabilizing force towards rare prey populations. The lower temperature treatment dampened the maximum feeding rate despite the higher attack rate. This indicates that the consumptive power of lionfish in invaded, cooler regions may be depressed through mediation of the handling time. When combined with the RIP metric, the importance of considering NR alongside FR is emphasised and gives credence to this new methodology. The predator abundance at 22°C (Cape Hatteras; Kulbicki *et al*. 2012) is relative to the abundance of lionfish in their native range in the Pacific and Indian Oceans, however the lower maximum feeding rate reduces the RIP to below that of the lionfish in the native range. This leads to questioning what other mechanisms are at play to cause such an excessive impact of lionfish on prey in the Atlantic. New information on lionfish

genetics has determined that the lionfish in the Atlantic invaded range (*P. volitans*) are actually hybrids of two species (*Pterois lunulata* and *Pterois russeli*) (Wilcox *et al*. 2017). Hybridization may have led to possible heterosis, which could be the key to the high abundance of lionfish in the Atlantic, and potentially a higher functional response than two origin species (Wilcox *et al*. 2017). However, it brings into account the reliability of comparisons between certain native populations and the invasive populations such as in Chapter 6, as the populations may be comparing two different species (Wilcox *et al*. 2017). Nonetheless, it could be determined that the impact of lionfish in cooler waters will be reduced and therefore making it less of a threat, but also that our comparative estimates for lionfish RIP in the Indian and Pacific Oceans (Chapter 6) are unreliable due to species hybridization and differences. Further, Barriche *et al.* (2017) determined the Mediterranean invasion population to be haplotypes of the Red Sea population. It is not known whether these are also hybrid individuals, if they are not it could potentially mean that the Mediterranean invasion will be of lower impact.

The lionfish was chosen as a case study of a successful invader and it is accepted that successful invaders often have a higher maximum feeding rate than native analogues (Dick *et al*. 2014; Dick *et al*. 2017a,b). The persistent high magnitude Type II functional response supports this theory and could be extrapolated that a future marine teleost invader will demonstrate these traits.

Variables of habitat complexity and light wavelength were investigated for their effect upon functional response parameters to provide a better story to explain the success of lionfish invasion (Chapter 2). Habitat complexity proved to have no significant effect on the functional response parameters. This is likely due to the lionfish utilising structures for hunting while the prey is utilising the same structure for refuge (Morris & Akins 2009). These experiments used a simplistic design and simplistic view to 'complexity', nonetheless the results indicate that further degrees of intricate complexity such as fractals and predator free space need to be considered (Jeffries & Lawton 1984; Barrios-O'Neill *et al*. 2014). Thus, management strategies of improving habitat complexity to provide prey refugia may be less effective, though contrasting reports from Belize suggest good quality habitat might be important in reducing impact (Hackerott *et al*. 2017).

Light wavelength is an important mediator of patterns in the marine environment (Cocheret de la Morinière *et al.* 2004), the discovery of populations of

lionfish on mesophotic reefs in the Atlantic invaded range (Kimball *et al*. 2004; Schofield *et al*. 2010; Nuttall *et al*. 2014; Andradi-Brown *et al*. 2017), has prompted concern at the idea that these damaging invaders could be taking refuge from managed removal techniques (Andradi-Brown *et al*. 2017). My results (Chapter 2) demonstrate the novel result that the maximum feeding rate is significantly reduced when under red light conditions, whereas blue and white light are somewhat similar. This suggests that the ecological impact of lionfish at these depths may be reduced by light wavelength mitigating the attack rate (Chapter 2). This could be combined, in a similar way to Chapter 6, to assess the RIP of lionfish at mesophotic depths using the abundance estimates from Andradi-Brown *et al*. (2017). Despite the lower abundance and *per capita* effect under red light/mesophotic depths, there are still inherent issues of lionfish colonising new areas. A recent report details how a mesophotic lionfish survey detected an undescribed fish species as it was consumed by a lionfish (Tornabene & Baldwin 2017).

The methods used in Chapter 6 could be used to further inform ecosystem models and predictions, such as the recent report by Chagaris *et al*. (2015) wherein predator – prey interactions and lionfish abundance is modelled for a 30-year period at an ambient temperature of 24°C, with reference to removal practices across different habitats. Chagaris *et al*. (2015) directly identify the lack of empirical information on the predation rate of lionfish under different scenarios and the uncertainty around these data while highlighting the importance of lionfish abundance as a driving factor in their impact.

While, a lionfish specific threat to NI fishery sustainability is unlikely, it is however likely that there will be increased marine invasions in the future by species that have similar traits but find the environmental gradient more optimal (Iacarella *et al*. 2015). Assessments of performance under different environmental variables is an informative way of pinpointing ways of mediating traits exhibited by damaging invaders (Barrios-O'Neill *et al*. 2014; Dick *et al*. 2014; Dick *et al*. 2017a,b; Laverty *et al*. 2017a,b).

7.3 Temperature specific findings

A trend across my findings was a lower attack rate with increasing temperature (Chapters 2, 3, 5). This is in contrast to meta-analyses that attack rate should not vary with temperature (Dell *et al.* 2011), however, it could be attributed to the study system investigated as there was a large body mass ratio in the predator-prey pairs investigated (Brose *et al*. 2008; Rall *et al*. 2009). MTE describes temperature as the main driver of biological patterns (Brown *et al*. 2004). This is based on the understanding that temperature mediates biological reactions, and thus controls metabolism which then affects physiological processes (Arrhenius 1889; Brown *et al*. 2004).

My results describe a variety of responses of handling time to temperature change. Lionfish (Chapter 2) and dogfish (Chapter 5) exhibited a lower handling time when temperature was increased (Chapter 2), this is in accordance with the expectations of MTE. It was an expected result in Chapter 2 due to lionfish being a tropical species and thus having a higher thermal optima (Kimball *et al*. 2004; Barker *et al*. 2017). In the context of NI fisheries and invasion into cooler waters, the predatory impact will be reduced under these conditions. Dogfish handling time showed a concurrent decrease with the raised temperature treatment, following the assertion that temperature is mediating metabolism and thus increasing hunger to replace metabolic energy losses (Li *et al*. 2017 (pre-print)) (Chapter 5). It could be considered if a higher temperature was investigated, that the handling time and therefore maximum feeding rate, would be negatively affected due to the possibility of a hump shaped relation with temperature (Englund *et al*. 2011; Rall *et al*. 2012; Fussman *et al*. 2014).

The handling time results in Chapter 3 (shanny) were somewhat disparate, the non-replacement model showed an increase in handling time when temperature was increased to 19°C, while 15°C and 17°C elicited similar handling times. The replacement model elicited low handling times at 15°C and 19°C. The differences in prey supply models are discussed in Chapter 3 and generally suggest that the results from the non-replacement model are reliable as long as they are taken as a relative comparative estimate, rather than absolute. The merits of replacement prey supply models are outweighed by the necessity for very high prey density treatments, more replicates, which in cases when prey supply is limited can be difficult to implement.

Further, the logistic difficulties in executing the replacement of prey at regular intervals negates the merit of the rapid and simple methodology found in non-replacement experiments with relatively little to be gained in reliability.

The results in Chapter 3, give support to the hump-shaped relationship of biological traits to temperature, wherein there is a thermal optima and peak, but also that species tend to live below their thermal optima (Martin & Huey 2008; Englund *et al*. 2011). My results indicate that predicted future temperature increases may actually be advantageous for prey populations due to the increased handling time and decreased attack rate at 19°C. Further, this is reflected in Chapter 6 wherein the RIP biplot metric and RIP_q calculations show a reduction in impact through reduction of predator population despite reduction of prey population.

There was an important result in the shift from a Type II FR to a Type III FR when temperature was increased (Chapter 3, Chapter 5). This shift was seen in both prey replacement models at 19°C in Chapter 3, along with a trend of decreasing maximum feeding rate with increasing temperature (Chapter 3), which could facilitate a low-density prey refugia at 19°C and thus protect the reduced prey population (Maranhão & Marques 2003). Contrastingly, dogfish showed a FR shift to Type III with thermal increase, but this also elicited a higher magnitude of FR with an increased maximum feeding rate (Chapter 5). I demonstrate that the movement to a more potentially prey stabilising FR could be beneficial to maintaining fishery sustainability, and as mentioned previously, higher temperatures could push past the peak of the temperature-feeding rate relationship to depress predation pressure (Chapter 3, Chapter 6).

7.3.1 Effect of thermal acclimation

The importance of thermal acclimation has been identified as a source of variation in the way species respond to thermal variation (Grigaltchik *et al*. 2012; Sentis *et al*. 2015). My results support this and expound upon the way in which differential treatment of predator and prey can act antagonistically or additively to change the maximum feeding rate of a predator (Chapter 5). Despite still coming under the umbrella of 'short term' experiments, these results prove the degree to which a week of thermal change and acclimation can affect feeding rates. The additive effect of concurrent thermal acclimation of both predator and prey on

maximum feeding rate is driven by the shorter handling time. When comparing this with the results from when only the prey was acclimated, the FR magnitude was lower than the ambient temperature baseline despite the attack rate being higher than when the predator was acclimated (Chapter 5). This confirms that in this case, raised temperature acclimation decreases attack rate or perhaps attack efficiency (Sentis *et al*. 2017). In this context, it is evident that there are complex mechanisms controlling predator – prey interactions under thermal change (Rall *et al.* 2009).

7.4 Diet of Irish Sea predators

I have detailed a comparative analysis of the diet of Irish Sea cod and dogfish (Chapter 4), in doing so I am contributing to informing the moving baseline of diet analysis. While there are obvious gaps in my data set, such as diel and temporal variation in prey consumption, this is a necessary exercise as it monitors shifts and fluctuations in the way consumers interact with resources over time (Borja *et al*. 2014). To understand the way in which interactions may change with climate change, it is important to first assess the present state in which the food-web is structured. I confirm that both species are generalist predators with a significant diet overlap in the Irish Sea (Chapter 4). I show that the high abundance of dogfish compared to cod is significant in that they are under exploited by fisheries (Richardson 2016), but exert considerable ecological pressure on prey populations (Chapter 4). With regards to substrate, there was little difference found in the way each species exploited different substrate matters, and survey design and analyses used do not account for predator movement and foraging between substrates (Chapter 4). Dogfish had heavier gut weight (I_F) than cod on muddy substrates. *Nephrops norvegicus* create their burrows in mud patches and are highly philopatric to these areas (Chapman & Rice 1971). Dogfish actively selected *Nephrops norvegicus* for prey, whereas cod did not (Chapter 4). However, it is unknown how much discard exploitation and consumption in the trawl net contributed to diet composition. Nonetheless, the percentage of dogfish diet made up by *Nephrops norvegicus* was high and therefore demonstrates resource exploitation by a non-commercial predator on an economically important prey species. This prompted the further investigation of dogfish FR, RIP and RIP_q in Chapters 5 and 6, wherein *per capita* response was quantified and combined with the numerical response, i.e. abundance to demonstrate

the importance of this growing predator population in the Irish Sea (Sguotti *et al.* 2016).

7.5 A new metric to assess impact potential under climate change

In Chapter 6 I provide a way in which an impact prediction method of invasive species can be adapted and improved to rapidly assess potential impact, and impact change, of species under predicted climate change scenarios. I address and build upon gaps acknowledged in the literature (Williams *et al.* 2008; Baum & Worm 2009; Van der Putten *et al.* 2010; Monaco *et al*. 2016; Stoffels *et al.* 2016), wherein *per capita* response, numerical response, predator and prey populations, and abiotic variables are combined in a simple yet effective metric. By correlating Equation 6.3 and Equation 6.4, I demonstrate that the results generated are equivalent, thus permitting the use of the simpler method (Chapter 6). This means that the methodology is more accessible to stakeholders and local management authorities to utilise, while still delivering reliable results. This is due to the simplicity, and not needing the standard deviations needed to calculate the pdf, which are sometimes not readily available.

The RIP biplots serve as a rapid graphical visualisation of impact potential, which is useful to observe uncertainties around the FR and AB estimations while being a comparative tool. Further, by incorporating the RRQ I demonstrate how the RIP metric becomes more informative and therefore useful, as both predator and prey populations and their response to temperature change can be taken into account with the RIP_q (Chapter 6). In some cases, there is no change, when in others there can be a decrease or increase in prey populations which then potentially changes the RIP to enhance or decrease it, which adds the necessary complexity to the calculation (Rall *et al.*2009, Gunderson *et al.* 2017).

7.6 Overall conclusions and applications

The data and results gathered in this thesis produce a complex picture of thermal responses and species interactions. While three predator species have been used as model systems; a successful invasive (lionfish), an abundant elasmobranch (dogfish) and a ubiquitous intertidal teleost (shanny), it remains important to caveat this study with the importance of species specific responses, as I demonstrate how

three species have differential responses to a variety of abiotic treatments. These are short term investigations, and thus will not be necessarily representative of long term population dynamics and species interactions (Jaksié *et al*. 1992).

The conclusions to be taken from this thesis revolve around the shift in FR Type with increasing temperature (Chapters 3 & 5) and the natural occurrence of a Type III response. These results indicate that when temperatures are raised the resource consumption of temperate predators change in a way that may confer protection to prey species due to low consumption at low resource density. This is likely related to changes in metabolic cost with increased temperature (Sentis *et al*. 2015) and the response of feeding rate to increased temperature (Lang *et al*. 2017). This has the potential of providing stability to prey populations under warming scenarios. However, this protection is limited to long term warming scenarios due to the hump shaped relationship with temperature increase (Chapter 3) (Englund *et al*. 2011). In the short term, moderate increases in daily mean temperature may serve to increase predatory impact (Vucic-Pestic *et al*. 2011; Sentis *et al*. 2017) (Chapters 3 & 5), which should be taken into account by stakeholders and policy makers.

The metric and methodology detailed in Chapter 6 are ideal for assessing potential impact and providing well rounded and supported evidence as to whether species pose a threat to resources. The information detailed in this thesis provides a limited view on species interactions under the context of climatic change. Nonetheless, the variety of results shown in this thesis point to a more complex relationship governing consumer – resource interactions. This compounds upon the importance of investigating thermal responses and other abiotic variables in a more complex manner, while continuing to monitor predator and prey population structure. The methodology used could be further utilised to assess interactions between species that occupy the same tropic level in order to understand effects such as competition and multiple predator effects on the functional response. Climate forcing is multifaceted and the many variables have both separate and interacting effects that could manifest in numerous ecologically relevant responses (Ferrari *et al*. 2014; Pörtner & Farrell 2008; Miller *et al*. 2015). This framework lends itself to the investigation of synergism and additive effects of multiple climatic variables due to taking into account the differential effects of variables upon both predator and prey population dynamics.

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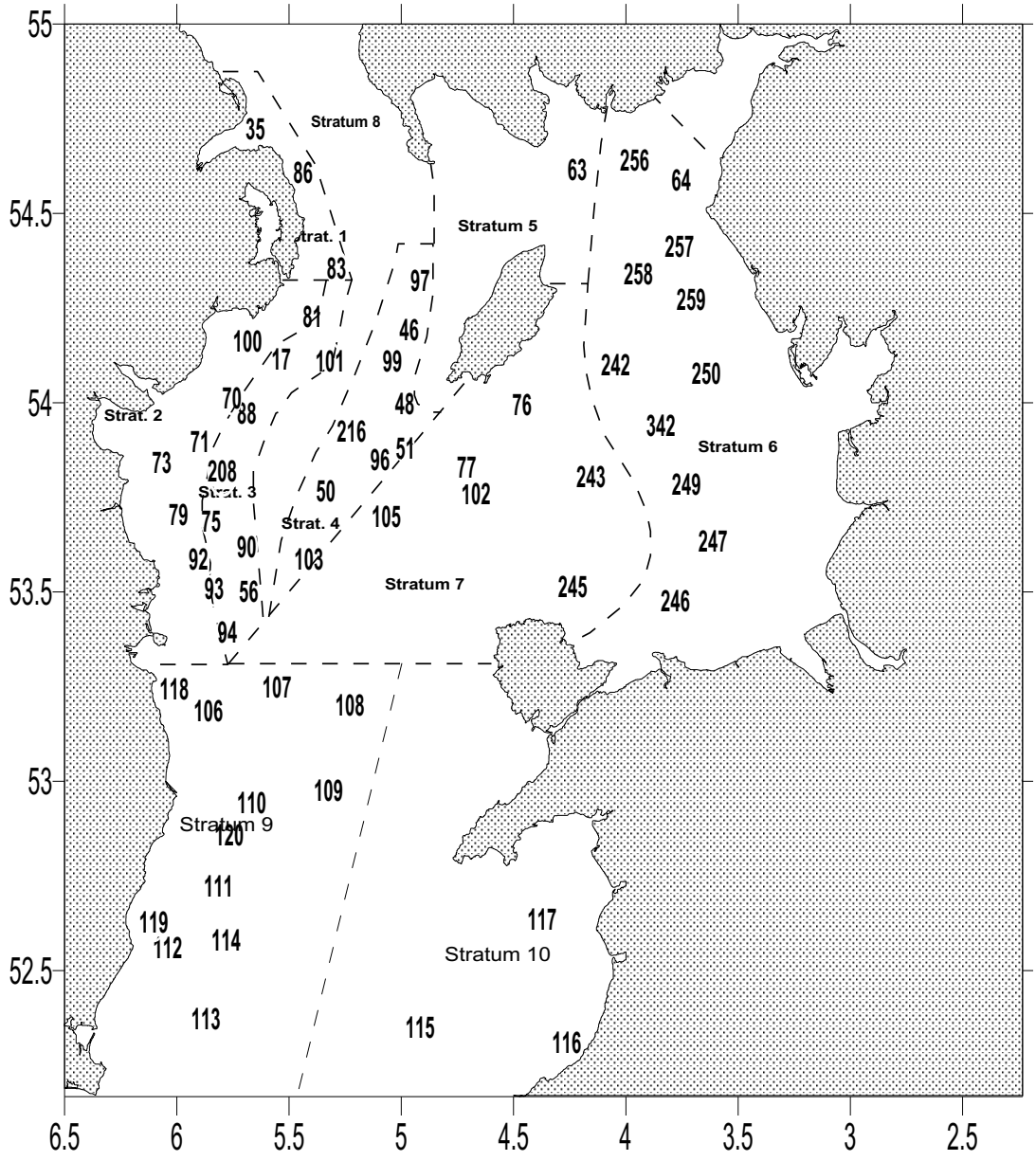
Appendix 1

Map of sampling stations and substrate types in the Irish Sea



Key to strata:
1. Irish Coast (N), <100m, Mixed sediments
2. Irish Coast, < 50m, sand and finer sediments
3. Irish Coast, 50 - 100m, Muddy sediments
4. W and SW Isle of Man, 50 - 100m, mud and muddy sand
5. N Isle of Man, <50m, gravel sediments
6. Eastern Irish Sea, <50m, sand and finer sediments
7. S. Isle of Man, <100m, gravel sediments
8. Deep western channel and North Channel >100m
9. St George's Channel west; sandy/mixed sediments; <100m
10. St George's Channel east; sandy/mixed sediments; <100m